The influence of upstream forest on macroinvertebrate communities in pastoral landscapes

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Abstract

The conversion of native forest to agricultural land has been an on-going issue threatening the health of New Zealand's freshwater systems. However, despite the fact that this has been occurring since early European settlement, our understanding of the mechanistic relationships between riparian vegetation and stream condition are poorly developed. This research investigated: (i) how forests affect downstream benthic macroinvertebrate communities in pasture and the environmental factors driving community change; (ii) how upstream forest size impacted the rate of change in downstream environmental drivers and associated macroinvertebrate community structure; and (iii) whether the addition of coarse particulate organic matter (a single potential driver of forest community structure) can reset community structure to that of a forested state. Physico-chemical conditions, basal energy resources, and macroinvertebrates were surveyed in several New Zealand headwater streams.

At Mount Egmont National Park, 10-12 sites were surveyed across a longitudinal forest-pasture gradient in each of five streams flowing from continuous forest to dairy farmland. My results showed that forests can have marked effects downstream. From the forest edge, water temperatures increased consistently, with a rise of approximately 0.2ºC per 100 m of downstream distance. By contrast, coarse particulate organic matter (CPOM) decreased rapidly downstream of the forest, however, low levels of "forest-derived" CPOM were still present 300m downstream from the forest edge. These environmental changes drove significant shifts in macroinvertebrate community structure. Moreover, pasture communities were markedly different from those in forest, despite being only 100 m from the forest edge. In particular, total macroinvertebrate and EPT richness and densities decreased, and communities shifted from evenly distributed allochthonous-based communities to autochthonous-based communities, highly dominated by molluscs (e.g., *Potamopyrgus* spp.)

Subsequent surveys of 6-8 sites across a longitudinal forest-pasture gradient in each of eleven streams flowing from forest fragments of different sizes into grazed pastures throughout the Canterbury region, indicated that stream temperature increased more rapidly downstream of small- and medium-sized fragments, than larger fragments. A Berger-Parker dominance index also indicated that macroinvertebrates responded principally to water temperature, with communities

being more highly dominated by temperature-tolerant molluscs in streams flowing from small-sized forest fragments.

Several headwater streams in Canterbury were also highly retentive, with marked CPOM rarely exported beyond 50 m downstream of the forest. Experimental additions of leaf litter to the pasture reaches of the same streams dramatically increased amounts of stored benthic CPOM. Although non-significant, trends indicated that EPT and shredder densities increased at litter addition sites, providing promise that CPOM can function as a mechanism directly enhancing healthy stream communities. My findings support the contention that when the replanting of entire stream reaches is infeasible, the use of riparian management strategies which focus on the planting of intermittent patches along stream banks can potentially improve stream habitat and community health downstream.

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Chapter 1: General introduction

1.1 Why are forests important for streams and communities?

Forest cover directly affects the physical environment of streams and rivers, and the biodiversity of the plants and animals that inhabit them (Fig. 1.1, Table 1.1). Only a fraction of light reaches the stream-bed due to interception by the riparian forest canopy and the surrounding topography, and absorption and scattering (attenuation) within the water column. High canopy shading also reduces fluctuations in stream water temperature and the maximum temperature attained by reducing inputs of solar and atmospheric radiation. New Zealand streams in forested catchments may have more than 90% shading and subsequently low water temperatures can be an important driver of forest community structure (Collier et al. 1995; Davies-Colley 1997; Quinn et al. 1997; Rutherford et al. 1997). For example, Quinn et al. (1994) reported that, in general, Plecoptera and Ephemeroptera are much less abundant in streams that have summer temperatures reaching above 19ºC and 21ºC, respectively. Additionally, shading reduces the growth of algae and other aquatic plants, including nuisance species such as the highly invasive macrophyte species *Egeria densa* and *Ceratophyllum demersum* (Champion & Tanner 2000; Reeves et al. 2004).

Forest vegetation also affects the morphology and substrate composition of streams by reducing the magnitude and frequency of flood events. A reduction in the number of floods reduces stream-bed and bank erosion, and therefore stream sediment available for transport is reduced. High stream-bed substrate heterogeneity is also often a reflection of low sediment inputs to forest streams and can result in an increase in habitat for aquatic plants, invertebrates and fish (Collier et al. 1995; Biggs et al. 1999; Niyogi et al. 2007). Furthermore, densely vegetated forest banks provide sites alongside streams and rivers where wet, rich, organic soils can intercept and denitrify contaminants from adjacent agricultural and urban land (Collier et al. 1995; Parkyn et al. 2003; Niyogi et al. 2007). Lastly, increased allochthonous inputs (such as leaf litter, woody debris and terrestrial invertebrates) from the forest, support stream assemblages and act as important food resources and habitats for in-stream biota (Parkyn & Winterbourn 1997; Nakano et al. 1999; Nakano & Murakami 2001; Lester et al. 2007). High levels of basal allochthonous resources and habitat diversity maintain healthy populations of lower order forest consumers, such as detritivores. This has a

wider implication for food web structure by fuelling a high biomass of secondary and top order trophic consumers such as freshwater predatory invertebrates, fish, and birds.

Forest structure along stream banks can have an important influence on a forest's effectiveness in maintaining ecosystem condition. Although very little work has been done to examine how riparian physical characteristics affect stream ecosystems, some international and New Zealand literature has shown that riparian buffer width (Spence et al. 1996; Nakamura & Yamada 2005), canopy density and height (Davies-Colley 1997; Rutherford et al. 1997), vegetation type (Parkyn & Winterbourn 1997) and the length of stream passing through a forest patch (Storey & Cowley 1997; Scarsbrook & Halliday 1999) can affect stream physical, biotic, and macroinvertebrate parameters (Fig. 1.1).

1.2 A brief history of forest loss in New Zealand

Forested landscapes encompass 4 billion hectares (31%) of the world's landmass (FAO 2010). However, forest loss, mainly through the widespread conversion of forest to agriculture, continues to have an important impact on global ecosystems with 13 million hectares of forest being lost annually in the last decade (FAO 2010). In New Zealand, human impacts on forest over the past 1000 years have eclipsed anything brought about by natural processes. Approximately 3,000 years B.P., 85-90% of New Zealand was covered in forest (Fig. 1.2), but the arrival of Polynesian settlers (*ca.* 1,000 B.P.) prompted widespread deforestation and subsequent ecosystem modification (McGlone 1989). The most extensive clearing of forest occurred suddenly, and over a short period of anthropogenic burning, between 750 and 500 years B.P. This period coincided with an increasing human population, the beginning of widespread pā (a fortified Maori village or settlement) construction, and dietary and cultural changes in Polynesian society, including increased cultivation of crops such as kumara (McGlone 1989).

By the time European settlers arrived in the early 1800s, approximately half of New Zealand's lowland forests had been removed (Stevens et al. 1988; McGlone 1989). Following European colonisation, the rate of deforestation in New Zealand accelerated (Arnold 1994). Extensive and rapid removal of lowland forest continued into the hill country driven by demand for land, timber and firewood (Stevens et al. 1988; Arnold 1994). Nineteenth-century New Zealand was a "wooden world" with wood used for anything from telegraph poles to shipping materials; in 1881, the vast majority of New Zealanders lived in a wooden dwelling (Wynn 2002). Clearance of primary forest continued throughout the mid twentieth-century;

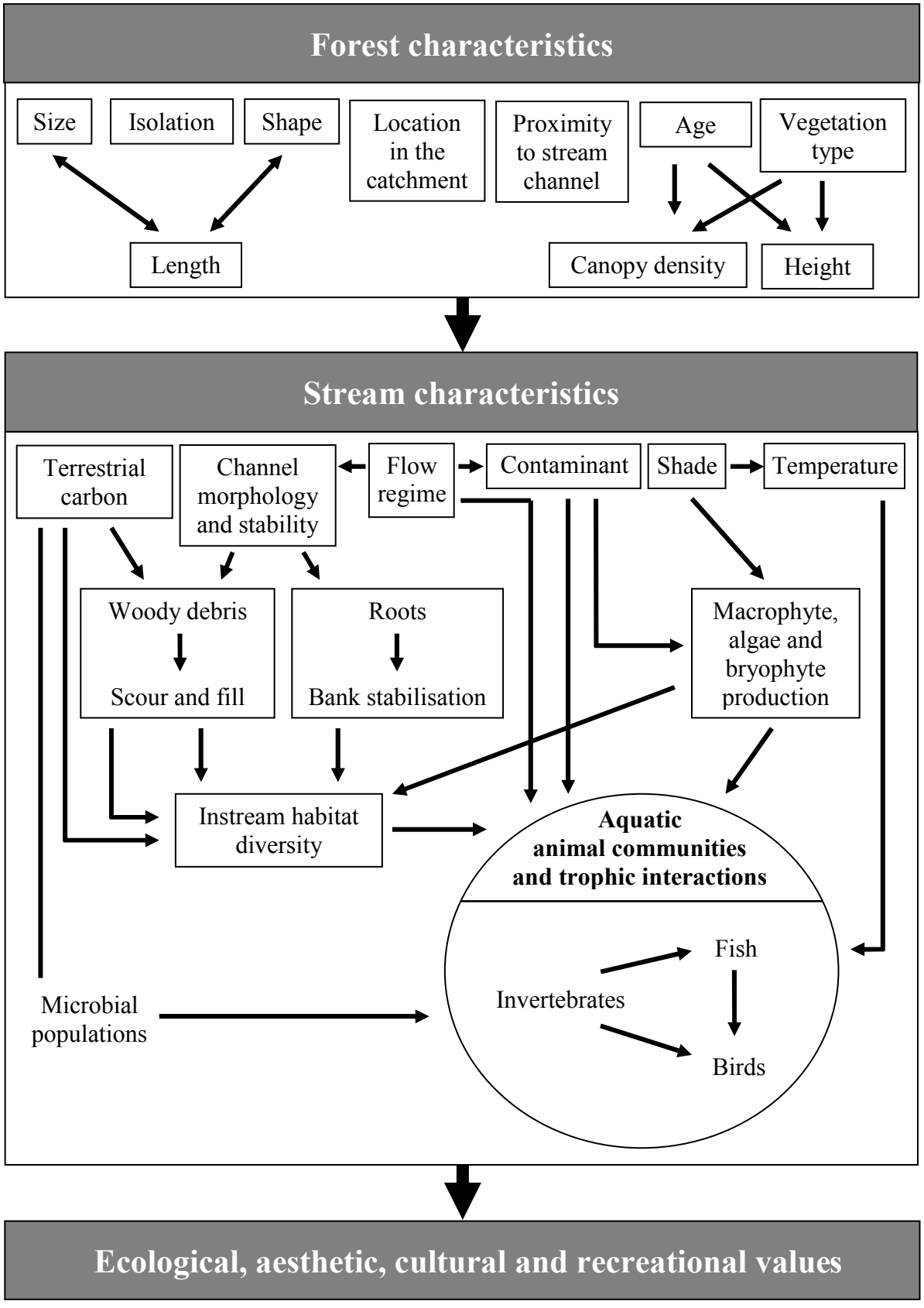

Figure 1.1 Potential interactions between riparian forest and its associated structural characteristics on lotic ecosystems. Adapted from Collier et al. (1995).

Table 1.1 Summary of riparian zone functions that potentially buffer streams from various land-use effects. Reproduced from Collier et al. (1995).

Riparian zone function	Potential in-stream effects
• Buffers banks from erosion • Buffers channels from localised changes in morphology • Buffers input of nutrients, soil, microbes and pesticides in overland flow • Denitrifies groundwater • Buffers energy inputs • Provides in-stream food supplies and habitat • Buffers flood-flows • Maintains microclimate • Provides habitat for terrestrial species • Maintains dispersal corridors	• Reduces fine sediment levels • Maintains water clarity • Reduces contaminant loads • Prevents nuisance plant growths • Encourages growth of bryophytes and thin periphyton films • Maintains lower summer maximum temperatures • Increases in-stream habitat features and terrestrial carbon inputs • Maintains food webs • Reduces flood-flow effects • Increases biodiversity

crops, pastures of introduced grasses, and exotic pine plantations displaced native vegetation from most of the lowlands, and many areas were completely cleared for mining, roading, and urban development (Fig. 1.2) (Wardle 2002). By 2005, only 31% (8.3 million ha) of New Zealand was left covered by forest, 78% being native forest held in the conservation estate and 22% being production forest (FAO 2006). Most of the nation's land is now used for agriculture, and deforestation is still occurring in parts of New Zealand (Norton 2000). However, the rate of indigenous forest loss has slowed, and forest regeneration is occurring in many parts of the country, such as Banks Peninsula and the East Cape (Harding 2003; FAO 2006).

1.3 The impacts of deforestation on lotic ecosystems

Hynes (1975) emphasised the strong link between terrestrial and aquatic environments stating "the valley rules the stream". What Hynes meant was that a stream's morphology, hydrology, water quality and biota are all influenced by external factors including geology and land-use activities occurring within its catchment. Internationally, much work has been done on the influence of land-use impacts on stream and river health (Nagasaka & Nakamura 1999; Heartsill-Scalley & Aide 2003; Danger & Robson 2004; Ferreira et al. 2005; Nessimian et al.

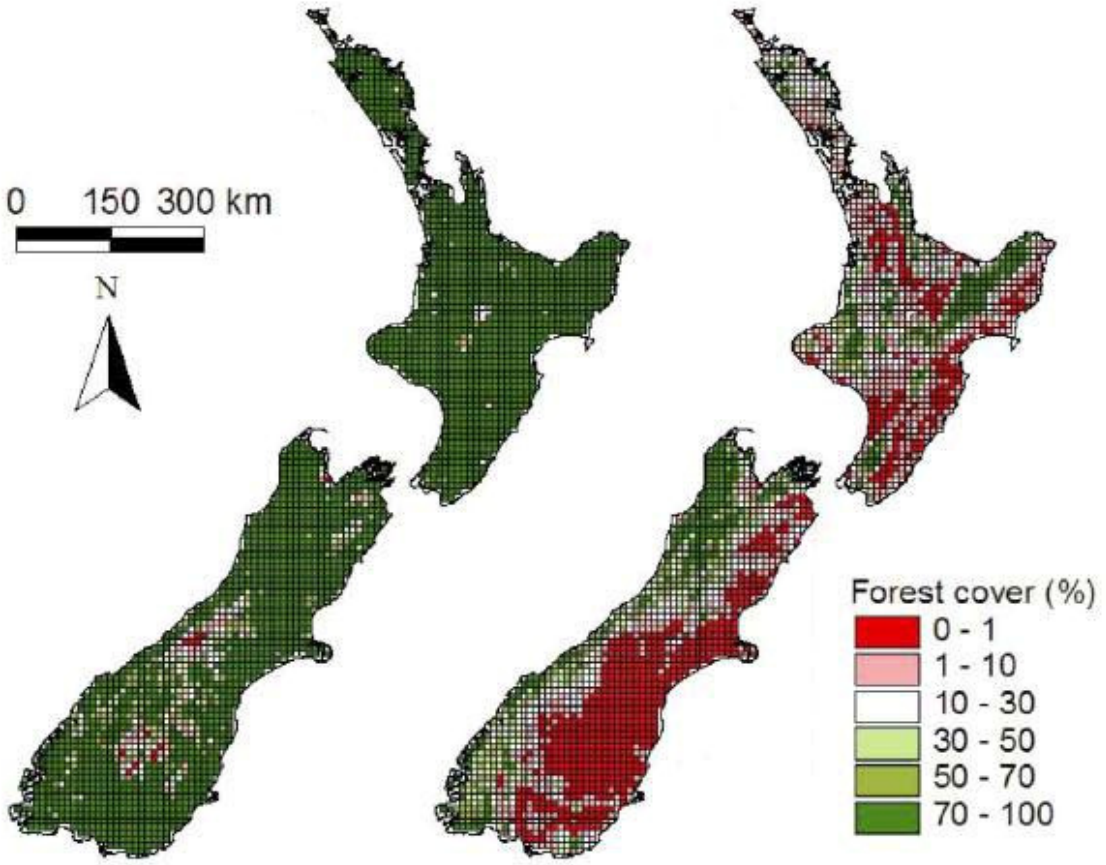

Figure 1.2 New Zealand forest cover before human settlement (left) and in 2002 (right) (Ewers et al. 2006).

2008). Benstead et al. (2003), for example, found that deforestation had negative effects on stream temperature, terrestrial organic resources, and macroinvertebrates in Madagascar, while Nakamura & Yamada (2005) obtained similar results in northern Japan. Habitat loss, such as that achieved through active deforestation, is recognised as the number one global driver of climate change and subsequent biodiversity loss (Millennium Ecosystem Assessment 2005).

The importance of land use activities and riparian vegetation for New Zealand aquatic ecosystems was recognised in early research (Phillips 1929; Allen 1959). Consequently, the influence of agricultural land-use activities has been considered to be one of the main factors influencing the health of New Zealand's freshwater systems (Smith 1993), and was described as the most significant environmental issue facing the nation (Upton 1994 in Scarsbrook & Halliday 1999). A number of New Zealand's endemic biota show strong preferences for forested conditions, but the extensive conversion of forest to agriculture has resulted in mass extinctions and declines, particularly of terrestrial species (Taylor & Smith 1997; Harding

2003; Ewers 2004). Over the past 900 years, humans have been largely responsible for the extinction of approximately 32% of New Zealand's endemic land and freshwater birds, 18% of endemic seabirds, and 42% of the country's frog species (Taylor & Smith 1997). In freshwater environments, only one fish species is known to have become extinct since the arrival of humans (McDowall 1990), however, it is difficult to predict how many others may have been lost or had their ranges severely reduced, and insufficient records exist to estimate the loss of invertebrate species (Harding 2003).

Management approaches to mitigate the adverse effects of deforestation and subsequent agricultural development on stream health and biodiversity have received increased attention in the last two to three decades (Collier et al. 1995; Quinn et al. 2001; Parkyn et al. 2003; Nakamura & Yamada 2005; Harding et al. 2006; Lorion & Kennedy 2009; Wilcock et al. 2009). A number of New Zealand studies have demonstrated the effects of agricultural and riparian land-uses on stream hydrology (Smith 1993), water chemistry (Maasdam & Smith 1994; Niyogi et al. 2007), sedimentation (Quinn & Stroud 2002; Niyogi et al. 2007) light and temperature regimes (Davies-Colley 1997; Rutherford et al. 1997), energy sources (Quinn et al. 1997; Townsend et al. 1997), and aquatic biota (Harding & Winterbourn 1995; Quinn et al. 1997; Townsend et al. 1997). However, many of these studies have focused on comparing catchments of differing land-use, rather than the effects of land-use change within the same catchment. Quinn et al. (1997), for example, showed differences in the water quality, habitat, and biota of eleven streams draining pasture, native forest and exotic pine forest in the Hakarimata Ranges, west of Hamilton. Specifically, Quinn et al. (1997) found that the largest differences in stream condition existed between native forest and pasture catchments; pasture streams were characterised by higher temperatures, nitrate levels, algal biomass, suspended solids, fine sediments, and invertebrate densities, but lower woody debris and EPT (Ephemeroptera, Plecoptera and Trichoptera) densities.

Storey & Cowley (1997) were among the first to investigate the recovery of stream communities flowing from pasture to forest in New Zealand. They sampled physical, chemical, and biological characteristics along three second-order pastoral streams that entered native forest remnants, north-west of Auckland. They found that 600 m within the forest, benthic macroinvertebrate communities had changed from that indicative of enrichment to a clean-water fauna in response to improvements in water quality, including decreases in stream temperature and nutrient enrichment, and increases in dissolved oxygen. Similarly, Scarsbrook & Halliday (1999) examined water quality, epilithon (algal biofilm attached to substrates), stream morphology, and aquatic invertebrates in three first-order,

pastoral streams flowing into native forest in the Waikato. They found that stream invertebrate community composition shifted to that characteristic of a native forest community just 300 m downstream of entering the forest. Despite these studies, there are considerable gaps in our understanding of the ecology of streams that flow from forest to pasture (Fig. 1.3).

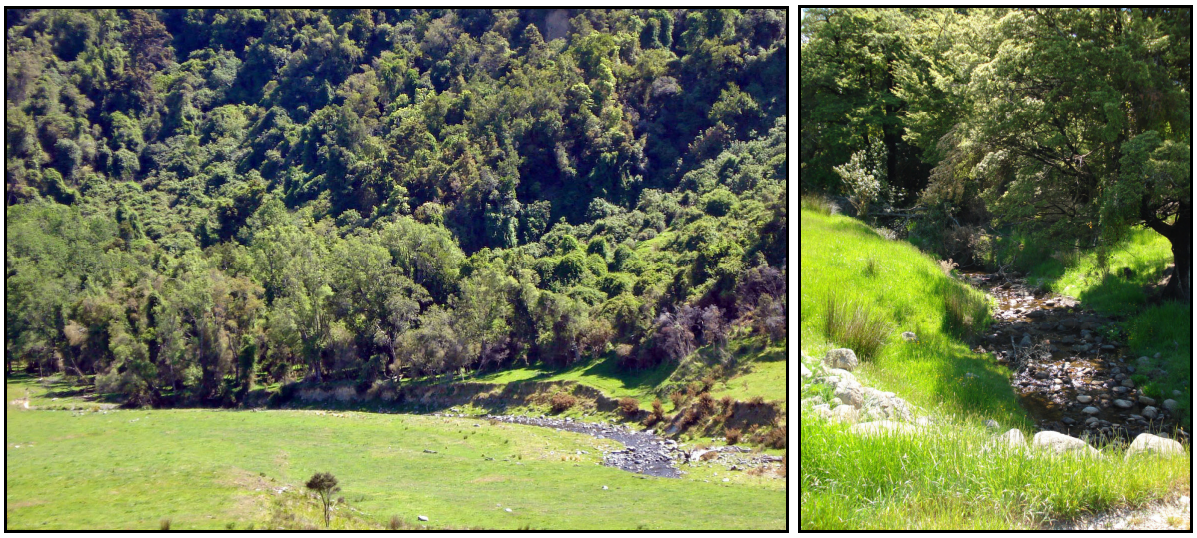

Figure 1.3 Two small streams flowing from native forest to pasture. The upper reach of the Motukaika River is a second-order stream in South Canterbury (left), and Flynn Stream is a first-order stream near Staveley, inland Canterbury (right).

Harding et al. (2006) expanded on ideas of longitudinal pasture-forest land-use impacts on streams by introducing the concept of a "forest reset effect". By definition, patches of forest embedded within agricultural landscapes were seen to have the potential to mitigate the effects of agriculture on stream water quality, and act as refugia and conservation reserves for aquatic species. Harding et al. (2006) stated that a forest reset effect may be brought about by improved shading, which can alter temperature regimes by reducing summer highs and moderating winter lows; stabilisation of banks, which can reduce sedimentation and turbidity; greater canopy cover and leaf litter fall, which can increase allochthonous inputs; and improved habitat and resource quality, which can shift benthic community structure towards more diverse assemblages. A forest reset effect might also be expected to persist downstream of forest for some distance as stream systems typically require space and time to respond to environmental changes. For example, time is required for solar energy to heat a body of water moving downstream, and forest-derived organic

inputs will be retained for some distance downstream. In practise, Harding et al. (2006) showed that forest fragments 5-7 ha in size did not mitigate the adverse upstream effects of pasture on stream conditions or the biota of two South Island streams. However, they noted that several factors might have influenced a potential reset effect, including; fragment riparian length, riparian forest width and vegetation type, and fragment location in the catchment.

A few studies have investigated the poorly understood influences of forest physical structure on stream conditions. Davies-Colley (1997) & Rutherford et al. (1997) found that the structural characteristics of riparian vegetation affected the efficiency by which forest maintains low stream temperature. Specifically, they showed that lighting of the streambed was controlled mainly by stream width in relation to the height and canopy structure of riparian vegetation. Besides these examples, very few studies have explored beyond the simple issue of forest versus pastoral land-use effects.

1.4 Riparian forest concepts relating to the management of streams and rivers

The health of our running waters and their biotic communities are valued for their ecological, aesthetic, cultural and recreational importance (Fig 1.1). The role of riparian vegetation in the maintenance of stream biodiversity has a key relevance to the management and restoration of New Zealand's agriculturally impacted streams and rivers (Collier et al. 1995; Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006; Wilcock et al. 2009). Essentially, this is because New Zealand persisted as a naturally forested landscape for millions of years and many of our endemic freshwater communities can be expected to be adapted to forested environments (Harding 2003).

In the past, introduction of shading has been seen as a major management strategy for controlling nuisance aquatic plants such as the highly invasive macrophyte species *Egeria densa* and *Ceratophyllum demersum* (Champion & Tanner 2000; Reeves et al. 2004). The potential for canopy shading to also reduce maximum stream water temperature could also be important for increasing community diversity as vastly fluctuating temperatures can have detrimental effects on stream communities (Quinn et al. 1994). Re-establishing forest vegetation could likewise improve the morphology and substrate composition of pastoral streams by reducing the number and severity of flood events. By reducing long-term stream sedimentation, stabilising banks and increasing stream-bed substrate size heterogeneity,

forests can improve the quality of habitats available for plants, invertebrates and fish (Collier et al. 1995; Biggs et al. 1999; Niyogi et al. 2007). Furthermore, replanting riparian vegetation can provide interception and denitrification sites for agriculture pollutants (Collier et al. 1995; Parkyn et al. 2003 Niyogi et al. 2007).

Invertebrate communities are particularly sensitive to environmental change and often provide good indicators of stream condition (Rosenberg & Resh 1993). As lower order trophic consumers, the structure of invertebrate communities has an important consequence for organisms higher up the food chain such as fish and birds. Trophic interactions are influenced by the amount of available basal food resources in an ecosystem and forest resources are often reduced in agriculture streams due to decreasing terrestrial leaf litter, woody debris and invertebrate inputs (Fig. 1.4). Reductions in terrestrial food resources, such as CPOM (coarse particulate organic matter), FPOM (fine particulate organic matter), and DOM (dissolved organic matter), are likely to lead to a reduction in the number of forest-adapted aquatic invertebrates, and along with reduced inputs of terrestrial invertebrates, have a cascading effect resulting in a potential reduction of predatory fish and birds (Fig. 1.4). Reduced woody debris in streams and rivers also reduces shelter, habitat diversity, and emergence sites for aquatic biota (Fig. 1.4). For example, Lester et al. (2007) showed that by experimentally adding wood to Australian streams, habitat complexity, and thus macroinvertebrate richness, could be increased.

1.5 The limitations to understanding how riparian forest can benefit stream ecosystems

The effects of riparian forests on freshwater ecosystems are dependent on stream physical structure and geographic scale, and the time-scale of stream processes within a catchment. Riparian vegetation will generally exert a larger influence alongside small headwater streams than large lowland rivers (Collier et al. 1995; Davies-Colley 1997; Rutherford et al. 1997). Furthermore, the benefits of replanting riparian zones may not always be immediate, and may take several years to become evident (Collier et al. 1995). For example, Davies-Colley (1997) and Trimble (1997) cautioned that the restoration of riparian canopy over pasture streams may carry the risk of increased bank erosion as sedimentary deposits, previously stabilised by pasture grasses and aquatic macrophytes which are removed, become destabilised during restoration activities and while the plantings become established. Furthermore, the structure of riparian forest has important consequences for stream condition. Specifically, riparian

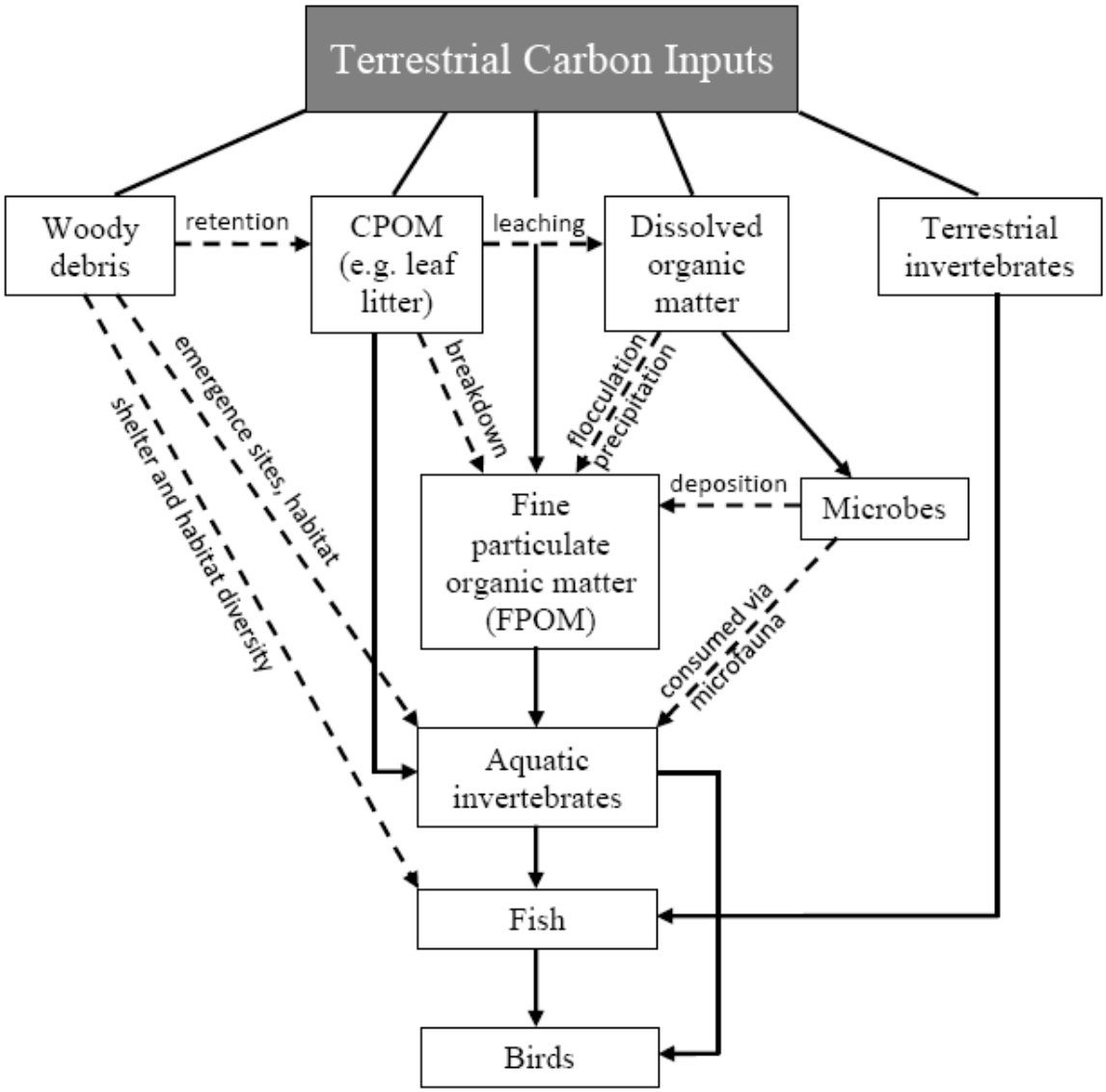

Figure 1.4 Major pathways (solid lines) by which terrestrial carbon sources fuel the production of aquatic invertebrate, fish and bird populations in stream and river ecosystems. Dashed lines represent interactions with various ecosystem processes (redrawn from Collier et al. 1995).

forest size, shape, length, structure and isolation, all products of historical deforestation that cause forest fragmentation, affect stream ecosystems in different ways (Fig. 1.1). The ways in which a forest's structural characteristics affect ecosystem function have been relatively well studied in a terrestrial context (Fahrig 2003), but similar studies are rare for freshwater ecosystems apart from a few overseas examples (e.g., Brazier & Brown 1973; Aubertin & Patric 1974; Spence et al. 1996; Nakamura & Yamada 2005).

Streams flowing from forest to pasture can be expected to undergo significant longitudinal change in abiotic and biotic parameters, including increases in sediment, algal biomass and temperature, and decreases in CPOM (Collier et al. 1995; Quinn et al. 1997; Scarsbrook and Halliday 1999). An important question to ask, therefore, is how far downstream do mitigating effects of forest last? In other words, can upstream riparian forest maintain forest stream conditions some distance downstream into pasture? It has long been asserted that forests indirectly benefit native stream community structure by driving abiotic and biotic conditions (Collier et al. 1995; Quinn et al. 1997; Scarsbrook and Halliday 1999). An important direction for management research now is to determine the functional mechanisms that bring about quantifiable, direct responses of freshwater biota to stream abiotic and biotic conditions. Knowledge of these mechanisms will have the potential to enable resource managers to maximise the benefits of riparian systems for the maintenance of freshwater biodiversity. Replanting riparian vegetation that target mitigating key abiotic and biotic conditions may have the potential to reset forest effects on stream communities much in the way Harding et al. (2006) hypothesized. The key to unlocking the nature of these mechanisms is through manipulating and isolating important stream abiotic and biotic drivers and directly testing community responses. Drivers are hypothesised to include terrestrial carbon inputs, channel morphology, flow regimes, shade and contaminant levels.

1.6 Thesis objectives

My thesis had three main objectives. The first objective was to investigate how forests affect downstream benthic macroinvertebrate communities, and to determine which environmental factors were responsible for altering communities. Second, I examined how upstream forest size impacted the rate of change in downstream environmental drivers and associated macroinvertebrate community structure. Lastly, I investigated whether the addition of CPOM (a single potential driver of forest community structure) functions as a riparian forest mechanism, mitigating the adverse effects of pasture on stream benthic communities.

The thesis is presented as four chapters, the first three being written as scientific manuscripts for future submission to peer-reviewed journals. The final chapter is an overall synopsis of my findings. I have attempted to keep repetition to a minimum; however, there is inevitably some overlap between data chapters, particularly in the Methods sections.

Chapter 2: *Do forests affect downstream macroinvertebrate communities?*
In this chapter, I describe a survey, which investigated the influence of upstream continuous forest on downstream macroinvertebrate community structure in pastoral land in five Mt. Taranaki streams. I compared my findings at several longitudinal sites upstream and downstream of the forest edge in order to determine the rate and magnitude of changes in benthic macroinvertebrate communities downstream from forest and to investigate the environmental factors driving these changes.

Chapter 3: *Does forest fragment size affect the magnitude and distance of a forest's effect downstream?*
Building upon patterns found in Chapter 2, Chapter 3 describes a study of streams flowing from different sized forest fragments. The aim was to investigate how forest size might affect the distance of any downstream change in communities.

Chapter 4: *Can the addition of organic matter modify pastoral stream macroinvertebrate communities?*
I investigated the rate of CPOM transport downstream from forests to test the importance of this subsidy on downstream communities. I put my findings in context with results from CPOM manipulations in pastoral streams, which I used to test whether CPOM can function as a mechanism mitigating the effects of pastoral intensification on stream benthic macroinvertebrate communities.

Chapter 5: *General discussion*
In this final chapter, I summarise my results within previous chapters and discuss these findings in the context of their potential for the restoration of agriculturally impacted stream systems in New Zealand. I also explore potential directions for the future study and management of agriculturally impacted streams and rivers.

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Chapter 2: Do forests affect downstream macroinvertebrate communities?

2.1 Introduction

The significance of catchment land-use for the condition and health of stream ecosystems has long been recognised (Phillips 1929; Allen 1959). Hynes (1975) coined the phrase "the valley rules the stream", emphasising this link between terrestrial and aquatic environments. In particular, forested landscapes encompass 4 billion hectares of land worldwide (31% of the global land area; FAO 2010) and have an important role in the ecology of streams and rivers. Forested streams typically have cool, clear water with low nutrient enrichment, diverse habitats, abundant allochthonous resources (i.e., terrestrial leaf litter, wood and invertebrates), and diverse communities, including some forest specialists.

Although some New Zealand studies have found geology to be important in determining water quality (Biggs 1990; Close & Davies-Colley 1990), land-use modification is often considered the main factor influencing the degradation of freshwater systems (Smith 1993; Maasdam & Smith 1994; Scarsbrook & Halliday 1999; Leland & Porter 2000; Quinn & Stroud 2002). Of particular importance, global deforestation, mainly through the conversion of forests to agricultural land, has occurred at a rate of 13 million hectares per year in the last decade, and 16 million hectares per year in the 1990s (FAO 2010). Historically, New Zealand followed this pattern of forest removal. Before Polynesian and European settlement about 900 years ago, 85% of New Zealand was covered by dense native bush (McGlone 1989; Taylor & Smith 1997; Ewers et al. 2006). Since then, widespread deforestation has cleared all but 15% of lowland native forest for use predominantly as agricultural land (Collier 1992). By 2005, only 31% of New Zealand was covered by a combination of exotic and native forest, 78% of which was protected (FAO 2006). This land-use change has had a significant impact on New Zealand's stream ecosystems, where riparian forest cover has been greatly reduced in many catchments throughout the country.

Conversion of forested streams to agriculture has been shown to cause marked changes in physical and biological conditions including: sedimentation and nutrient concentrations (Quinn & Stroud 2002; Niyogi et al. 2007; Song et al. 2009), light and temperature (Davies-Colley 1997; Rutherford et al. 1997; Harding et al. 1999; Young et al. 2005), hydrology (Smith 1993), channel morphology (Sweeney 1993), habitat heterogeneity (Allan & Flecker

1993; Harding et al. 1998; Townsend et al. 2003), basal energy resources (Quinn et al. 1997; Townsend et al. 1997; Benstead et al. 2003; Bojsen & Jacobsen 2003), and aquatic communities (Scott et al. 1994; Harding & Winterbourn 1995; Boulton et al. 1997; Quinn et al. 1997; Ometo et al. 2000; Hall et al. 2001; Harding et al. 2006). Almost all studies have shown that increases in agricultural intensity can have negative effects on water quality, stream habitat and benthic communities. Additionally, much research has shown both physico-chemical conditions and invertebrate composition change along "ecological gradients" of land-use change. For example, Harding & Winterbourn (1995) showed that physico-chemical habitat and invertebrate biota in first–third order streams changed with decreasing forest cover, from native beech (*Nothofagus* spp.) forest, to introduced (coniferous) forest, scrubland, and pasture in North Canterbury, New Zealand. They found pH levels were at their highest in scrubland streams, whereas taxonomic richness and density was highest in native beech forest, and molluscs were most prolific in pastoral streams (Harding & Winterbourn 1995). Other researchers have investigated stream physico-chemical, habitat and invertebrate responses longitudinally in pastoral streams returning to riparian forest. Scarsbrook & Halliday (1999) found that shade, channel width, and epilithon biomass in streams 300 m after entering native forest remnants were more similar to conditions found at a control forest site than within the pastoral landscape upstream. Furthermore, they found invertebrate community composition shifted towards the native forest condition 50 m into the forest and was the same as a forest community by 300 m.

Despite these studies, there are considerable gaps in our understanding of the ecology of streams that flow from forest into pasture. Specifically, we know little about the rate of physico-chemical, stream habitat and community change, or the extent and magnitude of this change. Ewers & Didham (2006) investigated forest edge effects in terrestrial ecosystems and defined the *magnitude* of an edge effect as "the difference between the maximum and minimum values of a response variable that is measured from the interior of the patch to the interior of the matrix habitat". In contrast, they described the *extent* of an edge effect as "the distance over which a change in the response variable can be detected". However, the uni-directional nature of streams mean that upstream processes are naturally transported downstream and we would, therefore, expect riparian land-use upstream to directly and indirectly affect subsidies in downstream reaches.

The aim of this study was to quantify the change (or magnitude of the forest edge effect) in physico-chemical conditions and macroinvertebrate community structure along an ecological gradient: from native forest, downstream into agricultural pasture where riparian

forest was absent. The focus of the research was to investigate the extent of the forest effect on unforested reaches, with particular focus on the environmental and biotic relationships that might drive changes in macroinvertebrate community structure. Firstly, I predicted that in-stream environmental parameters (such as temperature, substrate size, width and depth) and biotic conditions (including periphyton and CPOM (coarse particulate organic matter) biomass, and macroinvertebrate community structure), would change markedly along the forest–pasture environmental gradient. For example, I expected temperature to increase longitudinally downstream as shading from the forest canopy disappeared (Fig. 2.1a). Further, I expected a shift from allochthonous (CPOM and FPOM (fine particulate organic

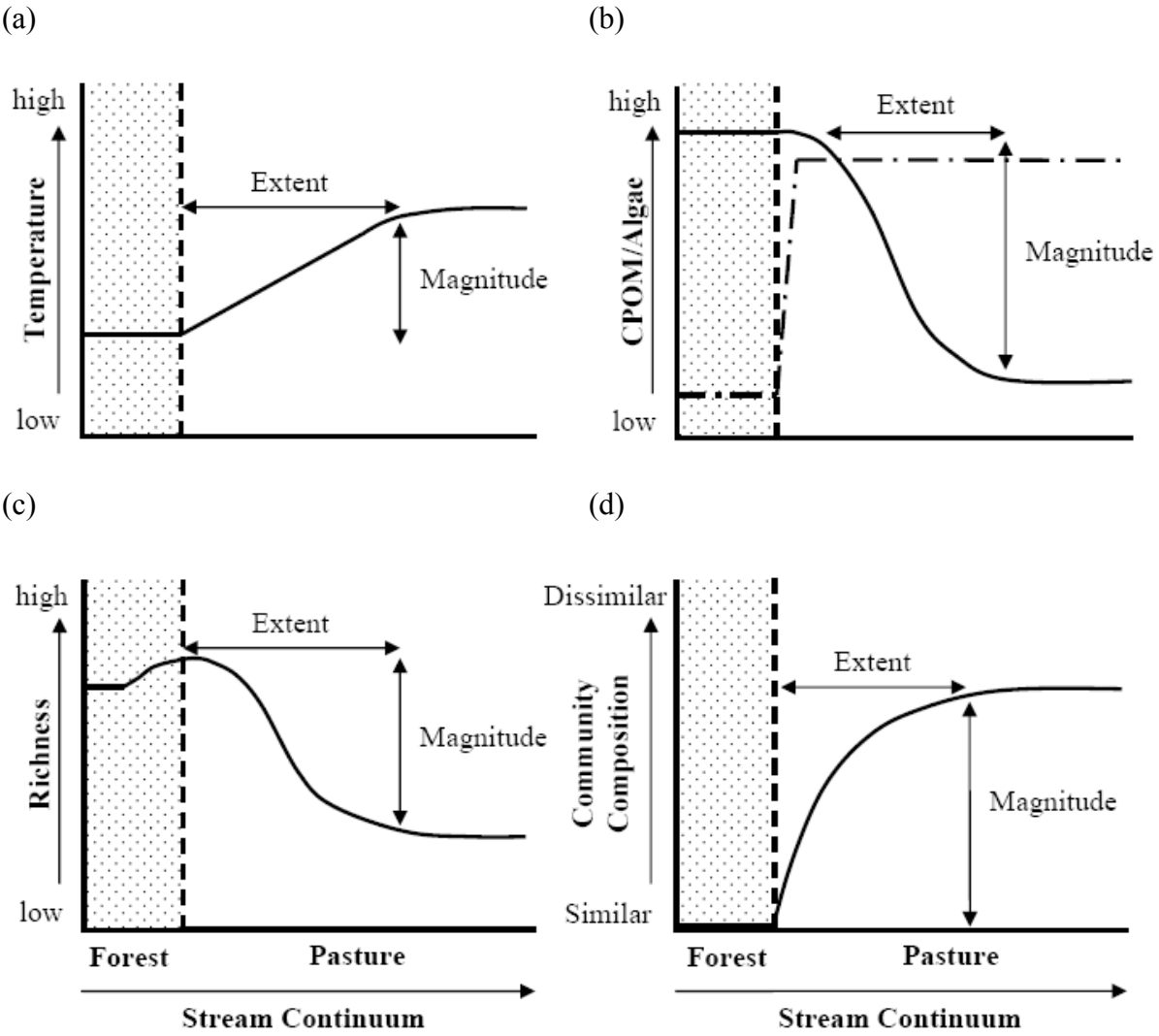

Figure 2.1 Predicted changes in the extent and magnitude of (a) physical variables, such as water temperature, (b) energy resources, such as CPOM (coarse particulate organic matter, solid line) and algae (broken line), (c) macroinvertebrate richness, and (d) macroinvertebrate community composition downstream of a forest edge into open pasture.

matter)) to autochthonous (algal) dominated food resources (Fig. 2.1b). In turn, this longitudinal change in temperature and the shift from CPOM dominated to algal dominated food resources was expected to have an effect on stream communities. Thus, taxonomic richness was expected to decline, because of the loss of sensitive forest specialists (Fig. 2.1c), and communities shift from shredder to grazing fauna (Fig. 2.1d). Secondly, I predicted that these environmental and biotic changes along the forest-pasture gradient would decline some distance downstream of the forest transitional zone (Fig. 2.1). This would likely be due to a forest-subsidy effect downstream (e.g. forest supplying organic resources to downstream reaches) maintaining a significant forest-edge effect.

2.2 Methods

2.2.1 Study site

The study was conducted on the edge of Egmont National Park, Taranaki, North Island, New Zealand. Egmont National Park encompasses 33,500 ha of volcanic land with Mount Taranaki (2,518 m a.s.l.) forming its nucleus from which many streams and rivers originate and radiate. Altitudinal and associated climatic patterns characterise the park's vegetation. At higher altitudes lowland and montane podocarp/broadleaf forests are replaced by small shrubs, which in turn give way to tussocks and herbs until, near the summit, only mosses and lichens grow to form scree communities (Clarkson 1986). Lowland forests cover more than half of Egmont National Park (> 16,765 ha). The most extensive type is rimu (*Dacrydium cupressinum*), rata (*Metrosideros robusta*) and kamahi (*Weinmannia racemosa* var. *racemosa*) forest, which occurs on the southern side of the national park where my study catchments were located (Fig. 2.2). Other dominant canopy species include mahoe (*Melicytus ramiflorus*), hinau (*Elaeocarpus dentatus*), miro (*Prumnopitys ferruginea*), toro (*Myrsine salicina*), tree ferns (*Cyathea smithii* and *Dicksonia squarrosa*), and large-leaved coprosma shrubs (*Coprosma grandifolia* and *C. lucida*) (Clarkson 1986). European settlers began converting the lowland slopes of Mt. Taranaki from forest to pasture over 150 years ago. As a result, there is an abrupt boundary at the park edge, where dense, mature forest within the park changes to a well-developed pastoral landscape (Fig. 2.2).

2.2.2 Survey design

Physico-chemical conditions and benthic macroinvertebrates were surveyed in five first-order streams in the late austral summer, from 5–10 March 2009. To control for the potential

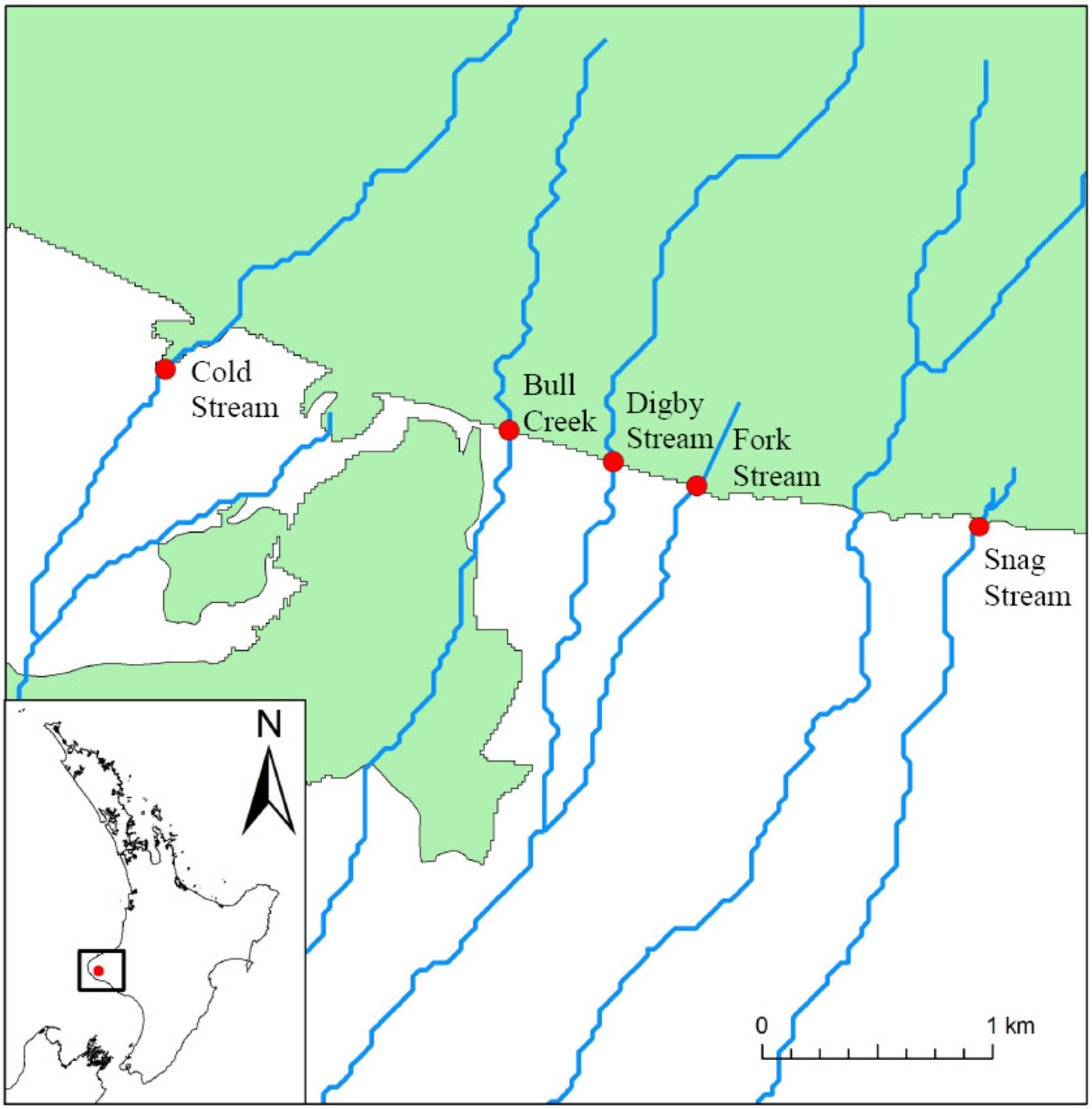

Figure 2.2 Locations of the five streams sampled on the edge of Mt. Egmont National Park. All streams (blue lines) flow from forest (green areas) into pasture (white areas) and red symbols indicate where physico-chemical and macroinvertebrate sampling was conducted at 3 sites upstream within forest, 1 site at the forest edge, and 7-8 sites in downstream pasture.

confounding effects of climate, location and elevation, all study streams were situated on the southern side of Mt. Taranaki, were close (< 4000 m) to one another and had similar elevational gradients (Fig. 2.2, Table 2.1). Furthermore, all forested sites were situated approximately 150 m within the national park boundary under a dense canopy of mature, native broadleaf forest.

Each of the five streams was sampled at twelve locations that ranged from continuous forest, to a pastoral dairy farmland. Three reach sites were located upstream within the continuous forest (-150 m, -25 m and -5 m), one at the forest-pasture edge (0 m), and eight sites downstream within pasture (2.5, 6.3, 15.6, 38, 98, 256, 612 and 1000 m). One of the study streams, Bull Creek, could not be sampled at 2.5 m because of extensive pooling of the stream channel, nor further than 612 m from the forest edge, as it re-entered native forest at approximately 650 m.

At each site, a range of in-stream physico-chemical parameters were measured. Dissolved oxygen (mg L^{-1} and percentage saturation; YSI 550A), temperature (ºC), pH and specific conductivity (μS_{25} cm^{-1}; OAKTON CON 10 series) were measured using standard meters, however, problems with these meters meant that the results for dissolved oxygen, pH and specific conductivity could not be used, and therefore only temperature was included in statistical analyses. Specifically, temperature was measured at early to mid-morning, before peak noon to mid-afternoon temperatures. Stream channel characteristics, including average depth, width and substrate size, were also measured. Average channel depth was calculated from three measurements at equal intervals across the stream. Stream width was measured across a representative section, and average substrate size was calculated by recording the length of the longest axis of 30 randomly selected particles at each site. Canopy cover was estimated from the centre of the stream channel using a densiometer (Forest Densiometers™, model-A).

Site location was recorded in the field using GPS (Garmin xTrexH) and several catchment scale variables were calculated for each site from stream and catchment datasets (NIWA 2004) using GIS (ESRI ArcGIS 9.3). These included longitudinal stream slope and elevation using a 25 m digital elevational model (Table 2.1).

The benthic macroinvertebrate community was surveyed at each site by collecting three Surber samples (0.0625 m², 250 µm mesh) from randomly selected riffles, and by taking a further single composite kick-net sample (250 µm mesh) from a range of microhabitats. Macroinvertebrate samples were preserved in the field in 70% ethanol.

CPOM (> 500 µm) was estimated at each site as the ash-free dry weight (AFDW) of all organic matter collected within the replicate Surber samples. AFDW of fine particulate organic matter (FPOM; < 500 µm) within the water column was also estimated from 1 L samples of filtered stream water, which were syringed in the field through glass microfibre filter papers (Whatman® GF/C, 1.2 µm pore size).

Table 2.1 Characteristics of the five streams sampled on Mt. Taranaki.

Stream	Distance from forest edge to final downstream site (m)	Location at forest edge (Easting, Northing)	Elevation range from forest edge to lowest site (m)	Stream slope (degrees)
Digby	1000	2599527, 6202198	420-390	3.5
Bull	612	2599316, 6201896	402-387	2.8
Fork	1000	2599780, 6202140	430-384	4.5
Snag	1000	2600973, 6201854	439-404	3.3
Cold	1000	2597233, 6202253	367-336	3.0

Periphyton biomass was estimated from three randomly selected stones (> 5 cm diameter). Stones were rinsed lightly under water, a 0.021 m^2 quadrat was randomly placed on their exposed surfaces (facing upwards into the water column from the stream bed), and the area within each quadrat was scrubbed with a small wire brush. The scrubbed algal matter from each cobble was then rinsed into a container with filtered water and syringed through filter paper (Whatman® GF/C, 1.2 µm pore size). Filter papers (FPOM and periphyton) were wrapped in tin foil and frozen within 8 h of collection.

2.2.3 Macroinvertebrate and organic matter sample processing

In the laboratory, Surber samples were sub-sampled due to very high macroinvertebrate densities. However, the entirety of each Surber sample was also scanned and any additional taxa not found in the sub-samples were added to the species lists, along with data from the kick-net samples. Each of the Surber sub-samples was rinsed thoroughly through a 250 µm-mesh sieve to remove excess sediments and its contents were transferred to a Bogorov tray for counting and identification, under a low-powered (10x magnification) dissecting microscope (KYOWA model sdz-pl). Macroinvertebrates were identified to species, where possible (Towns & Peters 1996; Smith 2003; Winterbourn et al. 2006). However, many early instars or damaged specimens lacked the necessary physical features to key them to species, and these individuals were instead classified to genus or family.

CPOM remaining in each sample was placed in foil weigh boats and dried, at 50ºC, for at least 48 h. Once dried, samples were ashed at 550ºC for 4 h and the average AFDW

(± 0.001 g) of CPOM was calculated for each site. FPOM samples were thawed at ambient room temperature, processed as per CPOM, and AFDWs (± 0.001 g) were calculated for each site.

2.2.4 Chlorophyll-*a* sample processing

Chlorophyll-*a* was extracted from the filtered periphyton samples in 30 mL of 90% buffered ethanol and magnesium carbonate solution (10 g of $MgCO_3$ and 1000 mL deionised water) for 12 h in the dark. Chlorophyll-*a* concentration was measured in very dim light, at room temperature, using a Trilogy™ fluorometer (model 7200-000). Each extraction sample was uncapped and 3 mL of solution added to glass test tubes with a pipette. To degrade the pheopigments, test tubes were removed from the fluorometer and 3 µL of 0.1 N HCL was added. After approximately 4-5 minutes, the raw fluorescence of acidified samples was measured. The same methods were performed on control samples containing ethanol only. Total chlorophyll-*a* was determined with the following formula:

$$\text{Chlorophyll-}a\ (\text{mg/m}^2) = R \times ((RFU_{before} - \text{control } RFU_{before}) - (RFU_{after} - \text{control } RFU_{after})) \times (\text{extract sample volume / sample area}) \times (1 / \text{dilution factor})$$

where R is a coefficient value that the fluorometer was calibrated to prior to analysis, RFU is raw fluorescence, and the dilution factor is the fraction of sample diluted from the original extract sample if raw fluorescence values were too high.

2.2.5 Statistical analyses

Linear mixed-effects (LME) models (using the *lme4* package in R version 2.9.2.; R Development Core Team 2009) tested with maximum likelihood (ML) were used to explore the amount of variation in stream physical, basal resource and macroinvertebrate variables explained by the fixed effect of distance downstream from forest edge (m) while accounting for variation due to differences among study streams (random factor). I used model simplification to estimate the *P* values and test the significance of the fixed effect, distance downstream of the forest edge. That is, distance was removed from the LME models and using ML, the Chi-square (χ^2) statistic and its significance level was estimated (Crawley 2007).

Macroinvertebrates were grouped into taxonomic orders and functional feeding groups (shredders, scrapers, collector-browsers, predators, herb-piercers and filter-feeders)

(Quinn et al. 2004; Mike Winterbourn pers. comm.). CPOM, FPOM, total macroinvertebrate density and scraper density data were log transformed, whereas EPT density, shredder density, mollusc density and Plecoptera density values were square-root transformed prior to analyses to meet assumptions of normality and homogeneity of variances.

To investigate whether macroinvertebrate community composition changed along the environmental gradient from forest to pasture, multivariate ordinations were performed in the statistical package CANOCO (version 4. 55; ter Braak & Smilauer 2006). An exploratory Detrended Correspondence Analysis (DCA) performed on log-transformed macroinvertebrate abundance data confirmed that the longest gradient length (2.98) fell under the gradient threshold (3.0; Leps & Smilauer 2003). This indicated that a Redundancy Analysis (RDA) was appropriate to analyse variability in macroinvertebrate community composition due to environmental drivers. Prior to an RDA ordination, I tested for collinearity among the 8 environmental variables using a correlation matrix in STATISTICA (StatSoft, Inc. 2009), but none were found to be highly collinear (i.e., $r > 0.9$). Thus, all environmental variables were used in the RDA including CPOM density, Chlorophyll-*a* density, FPOM density, water temperature, canopy cover, channel width, average depth, and average substrate size. The RDA explored macroinvertebrate community structure with the input of measured environmental stream predictors as driving forces. This analysis was performed on log-transformed macroinvertebrate densities to down-weight the influence of rare taxa.

To test the effect of distance on macroinvertebrate community composition, dissimilarity scores were calculated from the RDA axis 1 scores. That is, dissimilarity scores were calculated by subtracting each pastoral sample site axis 1 score from its respective stream forest centroid axis score (an average of all 3 forest axis 1 scores per stream; c.f. Didham et al. 2009). This gave an indication of community dissimilarity for each pastoral site, relative to forested community upstream (i.e., an indication of how different macroinvertebrate communities were downstream of the forest fragment). LME models were then used to examine whether community dissimilarity changed with distance downstream from the forest fragment. As before, I used model simplification and ML to estimate the χ^2 and *P* values to test the significance of distance while controlling for among-stream variation (random factor).

Finally, simple linear regressions using Poisson error distributions were used to directly test the effects of basal energy resources (i.e., CPOM or algal biomass) on the response of their respective functional feeding guilds (shredder and scraper densities,

respectively). A simple linear regression using a normal error distribution was used to test the effect of substrate size on algal biomass because no count data was involved.

2.3 Results

Some physical conditions varied with distance downstream from the forested reaches into the pasture sites (Fig. 2.3). Water temperature increased across all streams with increasing distance downstream from the forest edge by an average of 0.2º per 100 m (Fig. 2.3a, Table 2.2a). However, other physical conditions, such as substrate size, stream depth, and wetted width, did not change significantly with distance downstream (Fig. 2.3b-d, Table 2.2a).

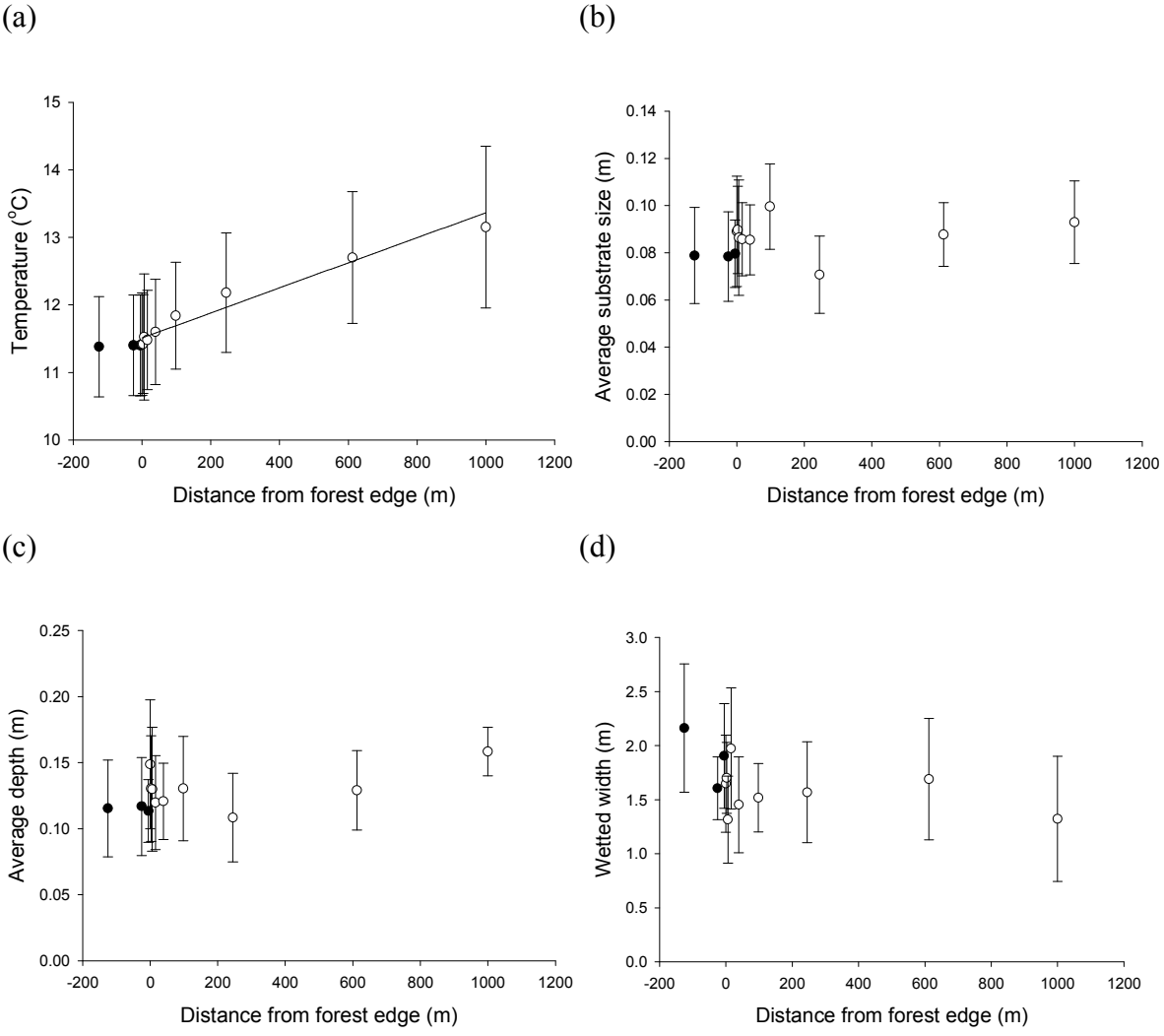

Figure 2.3 Mean (± 1 SE, *n* = 5) (a) water temperature, (b) substrate size, (c) channel depth, and (d) wetted width in streams flowing from continuous forest into pasture. Forested sites are represented by closed symbols and downstream pasture sites by open symbols.

Table 2.2 Mixed-effect model outputs for (a) physical, (b) biotic energy resource, and (c) macroinvertebrate responses with increasing distance downstream of the forest edge. Significant *P* values < 0.05 are indicated in bold.

Response	Effect variable	Variance	d.f.	χ^2	*P*
(a) Physical responses					
Temperature (ºC)	Stream (random) Distance	3.25	1	54.59	**< 0.001**
Average substrate size (m)	Stream (random) Distance	< 0.01	1	0.19	0.665
Average depth (m)	Stream (random) Distance	< 0.01	1	0.74	0.389
Wetted width (m)	Stream (random) Distance	0.73	1	0.14	0.706
(b) Biotic energy resources					
CPOM (g AFDM)	Stream (random) Distance	< 0.01	1	39.88	**< 0.001**
FPOM biomass (g/L)	Stream (random) Distance	0.02	1	1.25	0.264
Chlorophyll-*a* biomass (mg/m^2)	Stream (random) Distance	830942	1	3.51	0.061
(c) Macroinvertebrate responses					
Total macroinvertebrate richness	Stream (random) Distance	2.68	1	6.85	**0.009**
Total macroinvertebrate density (individuals per m^2)	Stream (random) Distance	0.06	1	25.83	**< 0.001**
EPT richness	Stream (random) Distance	4.92	1	9.25	**0.002**
EPT density (individuals per m^2)	Stream (random) Distance	7.71	1	5.13	**0.023**

Mollusc density (individuals per m²)	Stream (random)	86.35			
	Distance		1	39.35	**< 0.001**
Plecoptera density (individuals per m²)	Stream (random)	3.39			
	Distance		1	23.95	**< 0.001**
Shredder density (individuals per m²)	Stream (random)	< 0.01			
	Distance		1	18.13	**< 0.001**
Scraper density (individuals per m²)	Stream (random)	< 0.01			
	Distance		1	33.06	**< 0.001**
Community dissimilarity	Stream (random)	0.14			
	Distance		1	22.70	**< 0.001**

Coarse particulate organic matter (CPOM) showed an exponential decline from an average biomass of 48 g per m^2 at the forest edge, to less than 10 g per m^2 250 m downstream of the forest edge (Fig. 2.4a, Table 2.2b). Fork Stream showed the largest decrease in CPOM from 105 g per m^2 at 6.3 m downstream to 8 g per m^2 at 1000 m downstream. In comparison, FPOM (Fig. 2.4b, Table 2.2b) and periphyton biomass, as estimated by chlorophyll-*a* (Fig. 2.4c, Table 2.2b), did not change significantly along the forest–pasture gradient. However, some forest–pasture transitional sites (i.e., near the forest edge, 0–39 m) did show high levels of FPOM.

A total of 73 taxa were collected from the 58 sites (Appendix 1). Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies; EPT) accounted for 32.3% of all individuals and Mollusca (snails and other molluscs) 35.8%. EPT made up 64.6% of organisms at the forested sites, but only 27.8% at pasture sites. On the other hand, molluscs represented only 3.3% of individuals in the forest, but 40.4% across all pasture sites. Total taxonomic richness decreased with increasing distance downstream of the forest (Fig. 2.5a, Table 2.2c). Similarly, EPT richness (Fig. 2.5c) and EPT density (Fig 5d) decreased significantly along the environmental gradient from forest to pasture sites (Table 2.2c). Conversely, total macroinvertebrate density increased markedly downstream (Fig. 2.5b, Table 2.2c), probably because of the large increase in mollusc densities at distances greater than 98 m below the forest ecotone (Fig. 2.6, Table 2.2c).

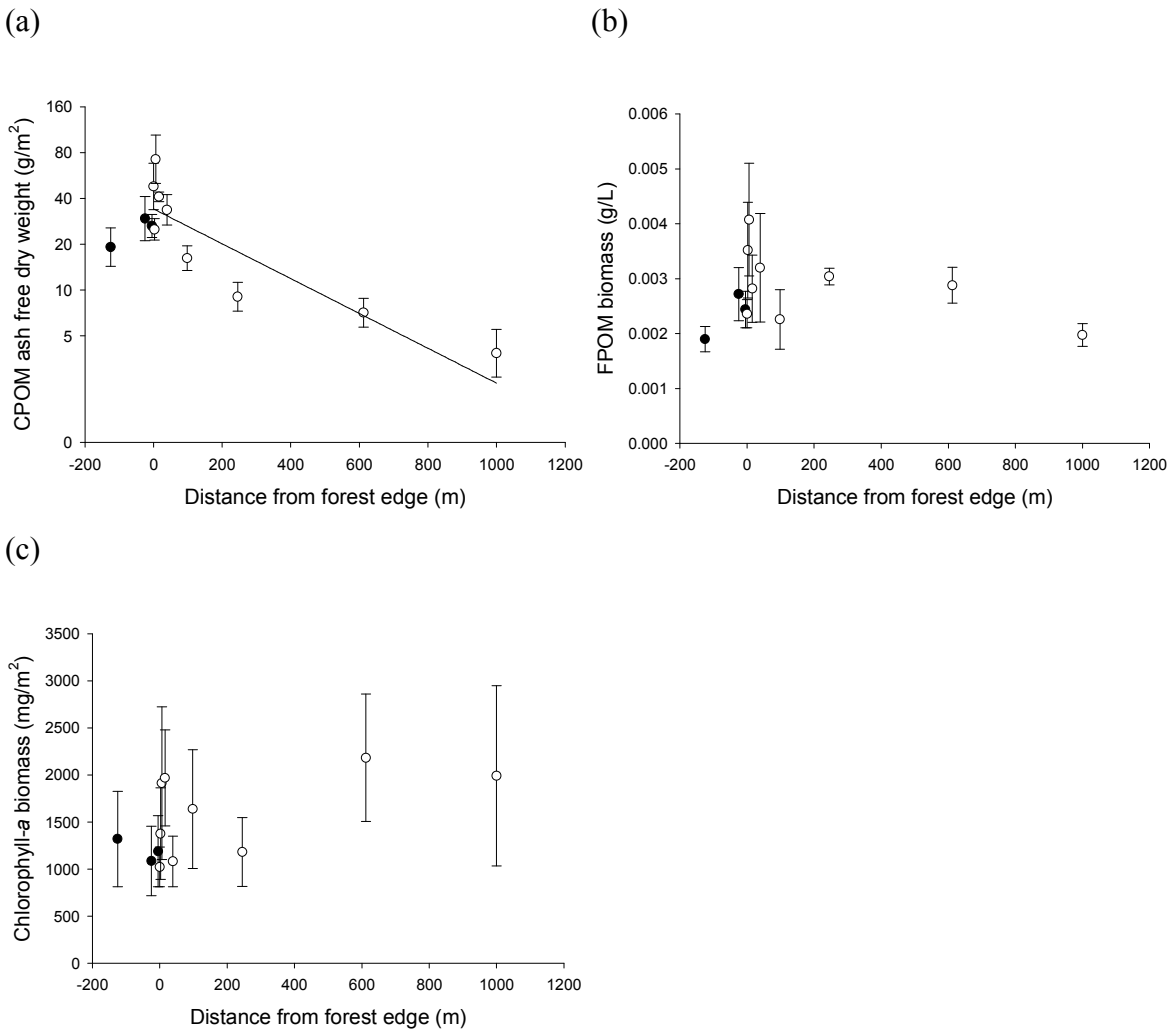

Figure 2.4 Mean (± 1 SE, *n* = 5) (a) coarse particulate organic matter, (b) fine particulate organic matter, and (c) chlorophyll-*a* in streams flowing from continuous forest into pasture. Forested sites are represented by closed symbols and downstream pasture sites by open symbols.

Functional feeding groups also changed over the longitudinal forest–pasture gradient. Shredder densities (e.g., *Austroperla cyrene and Paranephrops planifrons*) declined rapidly with distance downstream of the forest edge (Fig. 2.5e), whereas scraper densities (*Potamopyrgus* spp.) increased (Fig. 2.5f, Table 2.2c). The number of Plecopteran taxa also showed a significant decline with increasing distance away from the forest (Fig. 2.6, Table 2.2c)

An RDA ordination indicated that benthic macroinvertebrate community composition differed markedly between the upstream forested sites and downstream pasture sites (Fig. 2.7a). Axis 1 explained 11.3% of the variation in species data and 47.3% of the species-

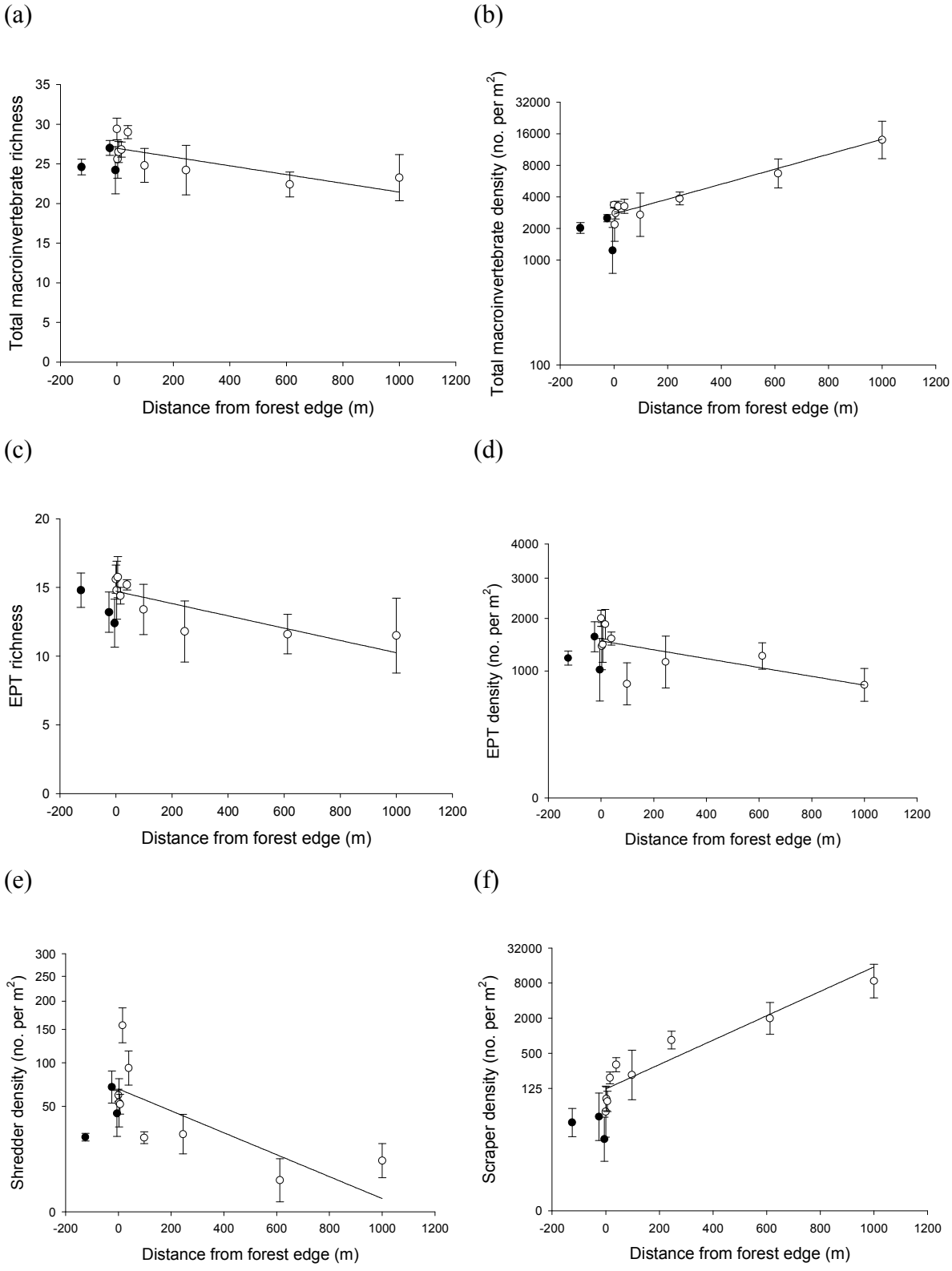

Figure 2.5 Mean (± 1 SE, n = 5) (a) total macroinvertebrate richness, and (b) density; (c) EPT richness, and (d) density and (e) shredder, and (f) scraper functional feeding guild densities in streams flowing from continuous forest into pasture. Forested sites are represented by closed symbols and downstream pasture sites by open symbols.

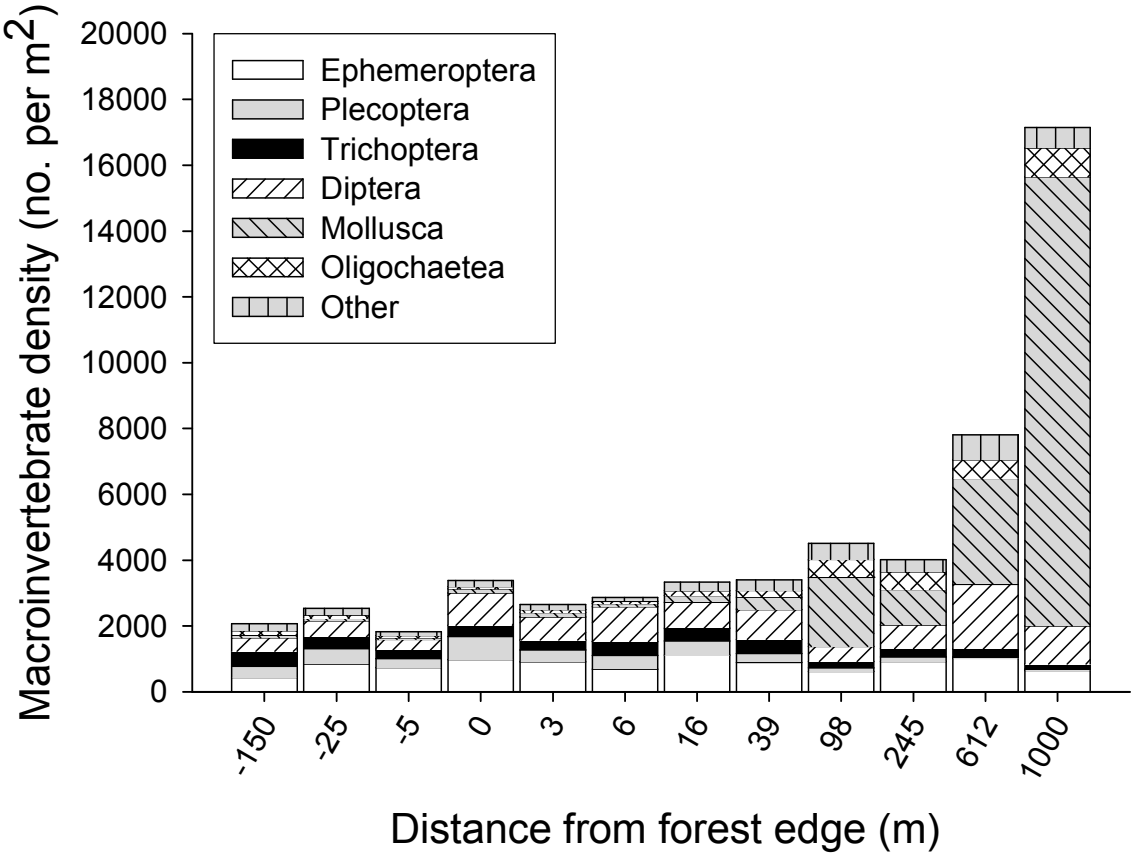

Figure 2.6 Mean densities of major taxonomic groups at distances downstream from the forest edge. Negative distance values are given for forest sites and positive distance values for pasture sites.

environment relationship variation. This latter effect was driven primarily by the higher CPOM biomass and greater canopy cover at the forested sites than the pasture sites. Axis 2 explained a further 6.8% of variation in the species data and 28.6% of variation in the species-environment relationship, the latter being driven primarily by differences in substrate size and water temperature. Collectively, CPOM, canopy cover, temperature and substrate size explained 75.9% of the variation among macroinvertebrate communities in forest and pasture sites. Much of this community change was the result of a shift from EPT dominance at forested sites to mollusc dominance at downstream pasture sites (Fig. 2.6 & 2.7b).

A comparison of community dissimilarity between pasture and forest over the longitudinal gradient indicated that macroinvertebrate communities changed rapidly below

the forest edge (Fig. 2.8, Table 2.2c). Specifically, communities just 39 m downstream of the forest were highly dissimilar to communities found in forested reaches (Fig. 2.8).

Functional feeding guilds showed inconsistent responses to changes in basal energy resources. As expected, shredder density increased with benthic CPOM abundance ($F_{1, 58}$ = 4.42, P = 0.040) (Fig. 2.9a), however, scraper density showed no significant relationship with chlorophyll-*a* biomass ($F_{1, 58}$ = 0.27, P = 0.607) (Fig. 2.9b). Chlorophyll-*a* biomass was significantly higher at sites with larger substrates ($F_{1, 58}$ = 41.40, P < 0.001) (Fig. 2.9c).

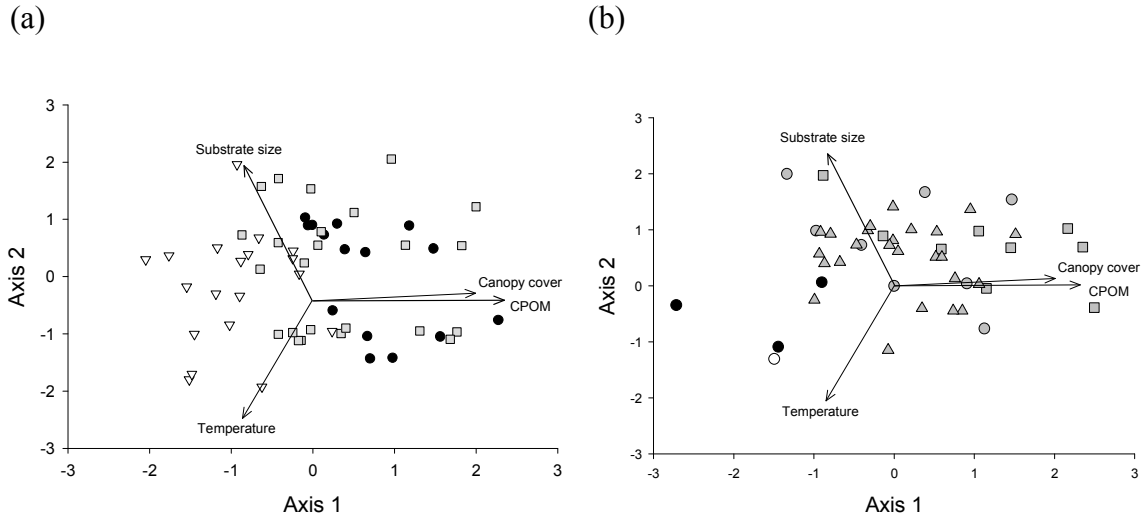

Figure 2.7 An RDA ordination for macroinvertebrate communities and significantly correlated environmental data collected at sites. Graphs show (a) site community structure in native forest (closed circles), within a 40 m transitional zone downstream of the forest edge in pasture (shaded squares), and at distances greater than 40 m downstream of the forest edge in pasture (open triangles); and (b) the associated five major invertebrate orders which structure each community (shaded symbols are EPT (Ephemeroptera = circles, Plecoptera = squares, Trichoptera = triangles), closed circles are Mollusca, and open circles Oligochaeta).

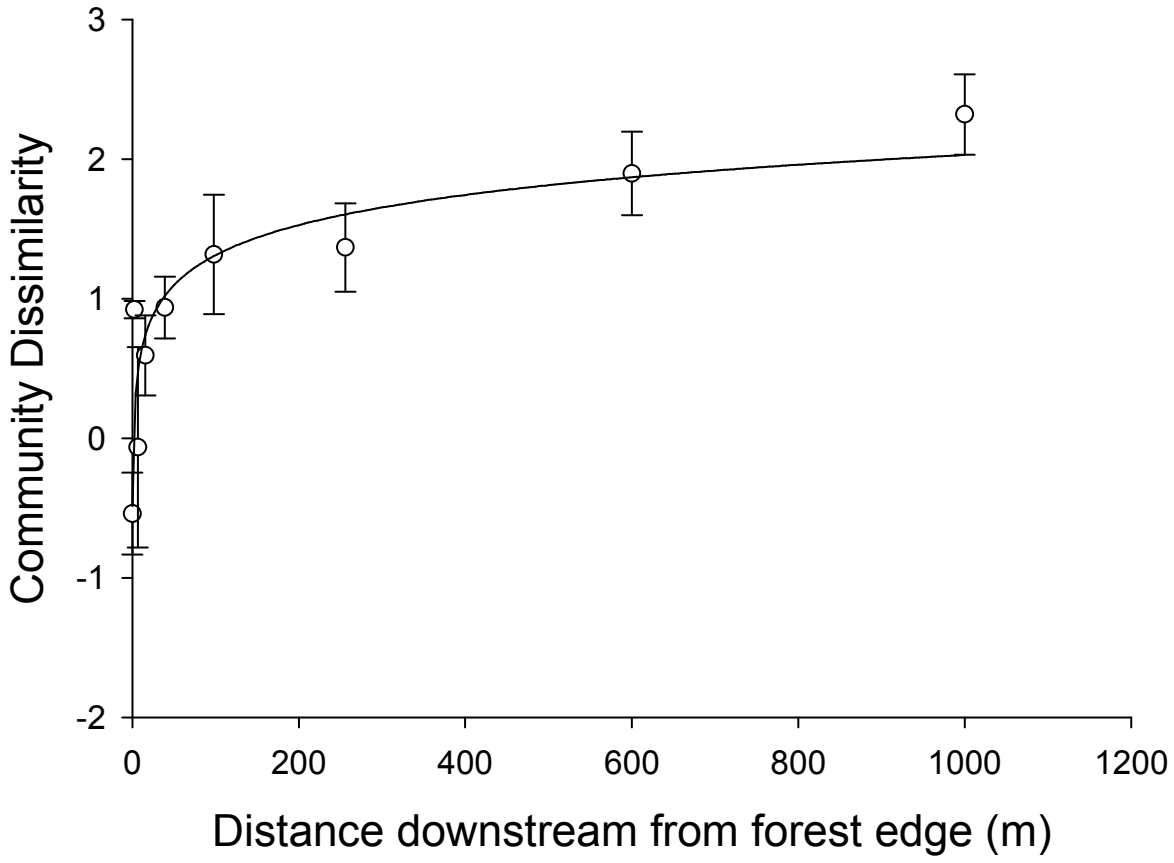

Figure 2.8 Mean (± 1 SE, *n* = 5) dissimilarity of macroinvertebrate community composition at pasture sites relative to forest reference communities. Reference forest scores were calculated as the average RDA axis 1 ordination score for the three forest sites on each of the five streams, individually. Pasture site axis 1 scores were then subtracted from the relevant forest score.

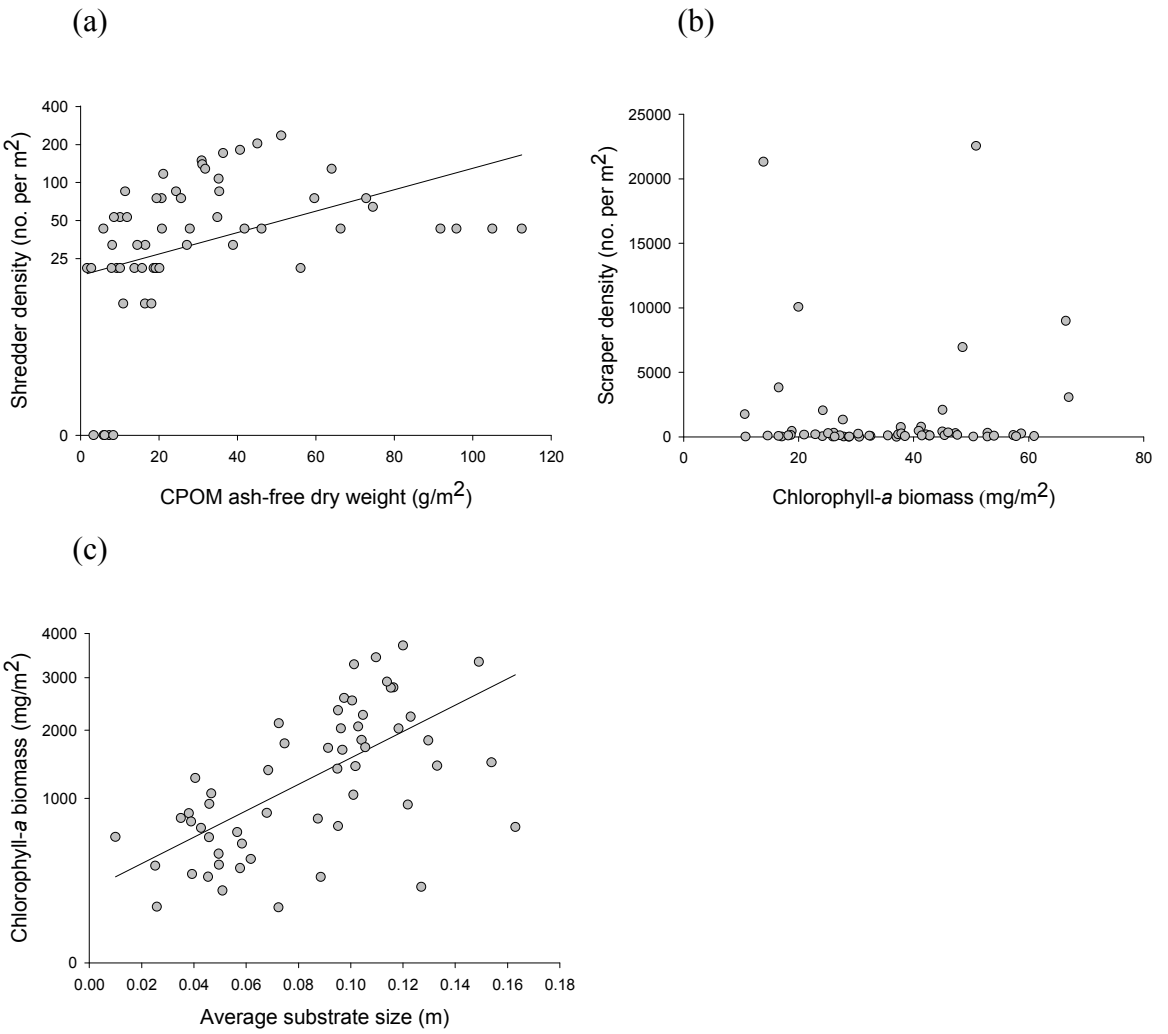

Figure 2.9 Functional feeding guilds compared with their respective energy resources; (a) shredder density and coarse particulate organic matter (CPOM; $r^2 = 0.16$), and (b) scraper density and chlorophyll-*a* biomass ($r^2 < 0.01$). Also shown is (c) periphyton biomass plotted against substrate size ($r^2 = 0.39$).

2.4 Discussion

Results largely confirmed my *a priori* predictions (Fig. 2.1) that abiotic conditions, biotic resources and macroinvertebrates would differ markedly from upstream forest sites, downstream into pasture. Specifically, temperature increased and CPOM biomass decreased longitudinally over this land-use gradient, from native forest into agricultural pasture. Furthermore, macroinvertebrate richness decreased with increasing distance downstream from the forest edge, whereas macroinvertebrate density increased. As a result, pastoral benthic communities became increasingly dissimilar from forest benthic communities with

distance downstream from the forest edge. These findings are generally consistent with those of other New Zealand studies that investigated the effects of longitudinal change in pastoral streams entering riparian forest (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006). However, contrary to my prediction, chlorophyll-*a* concentration did not increase significantly with distance downstream, and thus, there was no significant difference in periphyton biomass between forest and pasture sites. I also expected that environmental and biotic changes below the forest edge might show a lag effect due to a downstream forest subsidy effect, however, for many factors a subsidy lag did not occur.

Temperature in particular, showed a strong relationship with increasing distance downstream from forest edges in each of the five streams, and on average, it increased by 15% over the 1000 m below the forest edge. Storey & Cowley (1997) obtained comparable results for streams entering forest remnants in the Kaipara region, northwest of Auckland. They found that water temperature was highest where there was little forest cover, but declined rapidly upon entering the first 300 m of forest. Small streams are highly sensitive to direct inputs of solar radiation (Rutherford et al. 1997), and the increased riparian shade created by the forest canopy maintained low stream temperature. Lighting of a streambed is controlled mainly by stream width in relation to the height and canopy structure of riparian vegetation (Davies-Colley 1997). Several studies have shown that stream width narrows with agricultural intensification (Sweeney 1993; Davies-Colley 1997; Trimble 1997). For example, Davies-Colley (1997) found that pasture reaches of small New Zealand streams were half the width of forest reaches upstream. This narrowing could offset a portion of the expected temperature increase in pasture. However, stream width and depth did not change along my stream continua from forest into pasture. Similarly, Townsend et al. (1997) found that forested tributaries of the Taieri River in Otago did not differ significantly in width or depth from pasture or tussock grassland streams.

In addition to cool temperature, large boulders and cobbles often characterise forest stream reaches, whereas smaller substrates are characteristically found in pastoral streams (Hanchett 1990; Townsend et al. 1997; Heartsill-Scalley & Aide 2003). This difference could be due to variation in stream slopes (Heartsill-Scalley & Aide 2003) largely because forested streams are usually in mountains and pasture streams on plains. However, stream slopes were shallow over the entire environmental gradient in my study (min 2.8 degrees, Bull Creek; max 4.5, Fork Stream) and there was no significant change in substrate size between forest and pasture sites. Nonetheless, over the distance sampled in my study (up to 1000 m), I might

have suspected average substrate size to decrease because of an expected erosion of unstable pastoral stream banks adding fine silt to the streams.

Biotic resources along the longitudinal gradient were also predicted to change markedly. For example, the change from a dense native canopy to an exposed open stream might have been expected to result in a shift from allochthonous (e.g. leaves and woody debris) to autochthonous (e.g. algal) basal food resources. Compared to the results of previous studies, which have shown this effect among separate forested and pastoral streams (Quinn et al. 1997; Heartsill-Scalley & Aide 2003), I obtained variable results. Benthic CPOM showed exponential declines downstream, with high biomass at forest and transitional sites near the forest edge. Specifically, streams displayed an almost total loss of CPOM further downstream (presumably because the only source of CPOM was from the forest). The effect was a loss of up to 100 g per m^2 of CPOM by 300 m downstream of the forest-pasture transition. Similarly, Scarsbrook & Halliday (1999) showed that mean CPOM dry mass was higher at forested sites than pasture sites in first-order, hill-country agricultural streams entering forest remnants in the Waikato.

Contrary to prediction, my study showed periphyton biomass did not differ significantly between pasture and forest. Elsewhere, low epilithic biomass has been observed in pastoral streams near Hanmer in the South Island of New Zealand (Harding & Winterbourn 1995) although the reason for this was unclear, and the authors suggested that dense grasses in the stream channel may shade the streambed. Alternatively, high sedimentation, and thus reduced water clarity, may have inhibited periphyton growth. My study streams in Taranaki exhibited little sedimentation, however, and were not overgrown by pastoral grasses. In contrast, periphyton biomass increased with increasing substrate size, but variable substrate size did not differ significantly between pasture and forest. Therefore, a potential explanation for my results is that substrate size was small enough in both forested and pasture reaches to be affected by disturbances, such as high flows, which would have inhibited periphyton growth over entire stream continua. Biggs et al. (1999) found that flood flows and bed movement greatly reduced periphyton biomass in South Island, headwater streams. Water column FPOM also displayed no significant pattern over the forest-pasture land-use gradient. Nevertheless, some sites did show high levels of FPOM near the forest, and all pasture sites showed low to medium levels.

Macroinvertebrate indices showed significant change in response to the forest-pasture gradient. While total macroinvertebrate and EPT richness decreased significantly with increasing distance away from the forest, total benthic macroinvertebrate density showed a

significant increase with increasing distance into pasture. Quinn et al. (1997) reported invertebrate densities 3-fold higher in pasture than native forest streams. In both my study and that of Quinn et al. (1997), this increase in density was attributable to increases in molluscs. In contrast, EPT densities were considerably lower at sites far from forest margins relative to those close to forest margins. This is consistent with the typically low tolerance of EPT taxa to pastoral conditions. For instance, Quinn et al. (1994) reported that in general, Plecoptera and Ephemeroptera are much less abundant in streams that have summer temperatures reaching 19ºC and 21ºC, respectively. However, study stream temperatures in this case never reached above 15.5ºC at the time of measurement (morning, late summer).

Changes in macroinvertebrate assemblages over the forest-pasture gradient highlight the significant shifts that occurred in overall community composition. Pasture communities were substantially different from those at forested sites 100 m downstream, whereas transitional sites within 40 m of the forest were more similar. These findings indicate that forest loss and a subsequent shift from primarily allochthonous- to primarily autochthonous-based communities, leading to community simplification (loss of species), can be driven largely by biotic processes. This has been suggested by Benstead et al. (2003), and Benstead & Pringle (2004), for deforested tropical streams in Madagascar. Specifically, shifts in the relative importance of basal food resources between stream reaches in agricultural versus forest land-use types, can cause a change in the relative abundances of the specialised species that feed on them. As previously highlighted, CPOM biomass and shredder density both showed significant responses to distance downstream of forest edges. Evidence that biotic processes were largely responsible for driving community structure was supported by the strong link between CPOM density and shredder density. An RDA ordination likewise indicated that CPOM density was the primary predictor of community structure followed by canopy cover, temperature and substrate size. Townsend et al. (1997) obtained similar evidence suggesting that shredders were more abundant in native and introduced forest than pasture reflecting the availability of detritus. Furthermore, Hicks (1997) used stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) in several Waikato streams to show that food webs in forest streams were based on allochthonous materials, whereas food webs in pasture streams appeared to be based on a mixture of allochthonous and autochthonous resources. Although scrapers (predominantly molluscs) contributed to the change in community structure downstream of forest, their dependence on changes in periphyton biomass was not apparent. Isotope analyses could be a useful tool to help develop and understand the relative

importance of allochthonous versus autochthonous food-resources along a longitudinal forest-pasture gradient.

It is also important not to ignore the impact of abiotic drivers of community change. Temperature was a primary driver of community structure along ordination axis 2, and as previously mentioned, Quinn et al. (1994) found that certain taxa are highly sensitive to thermal regimes. High temperatures increase the metabolic rate of stream dwellers, but decrease dissolved oxygen concentrations (Quinn & McFarlane 1989) thereby adversely affecting stream communities. Additionally, nutrient and sedimentation impacts on streams have frequently been shown to be markedly higher in pastoral rather than forested streams (Quinn et al. 1997; Scarsbrook & Halliday 1999; Niyogi et al. 2007) and it is generally considered that EPT taxa are sensitive to organic enrichment (Scarsbrook & Halliday 1999). My study was limited by the inability to measure these effects.

In conclusion, stream macroinvertebrate communities change longitudinally along forest streams flowing downstream into pasture. This change begins within transitional zones near forest boundaries where diverse forest communities (with high EPT and shredder richness and densities) shift along a continuum to become pastoral communities (with low EPT richness and density, and high scraper density). About 100 m downstream of the forest edge, the pastoral communities I studied became very different from those found in the forest. This shift occurs as a response to rapid modifications in both stream biotic processes and habitat below native forest boundaries, predominantly changes in the availability of terrestrial food resources and in thermal regimes. Investigating these drivers as mechanisms of community change requires further study. Ecologists should aim to test the responses of stream communities to changes in biotic and thermal drivers by isolating their effects through experimental manipulation in the field and laboratory. By examining the mechanistic linkages between community structure and riparian zones, resource managers and resource users may attain the information required to mitigate adverse effects of pastoral land use. In this way, they may target riparian management strategies that maximise key mechanistic processes, which benefit stream ecosystems including the organisms that reside in them.

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Chapter 3:
Does forest fragment size affect the magnitude and distance of a forest's effect downstream?

3.1 Introduction

Habitat loss and fragmentation caused by land-use change, have pervasive and negative impacts on biodiversity (Millennium Ecosystem Assessment 2005). The direct effects of habitat loss *per se* are often considered to pose the greatest threat to the maintenance of species (Tilman et al. 1994; Dobson et al. 1997; Sala et al. 2000; Ewers & Didham 2006a), and negatively impact species richness, population abundance and distribution, and genetic diversity (Fahrig 2003). Research has also shown habitat loss to have negative impacts on indirect measures of biodiversity and factors affecting it such as population growth (Bascompte et al. 2002), trophic chain length (Komonen et al. 2000), species interactions (Taylor & Merriam 1996), breeding success (Kurki et al. 2000), dispersal success (With & King 1999; Belisle et al. 2001), predation rates (Bergin et al. 2000), and foraging behaviour (Mahan & Yahner 1999).

The widespread clearance of forest is a key example of habitat loss, and its effects on ecological communities have been well-documented (Hinsley et al. 1995; Hargis et al. 1999; Gibbs 1998; Fahrig 2003; Ewers & Didham 2006a). Global deforestation continues to occur at alarming rates, with 13 million hectares of forest being cleared worldwide each year (FAO 2010). Historically, New Zealand was almost completely forested below the alpine treeline (Ewers 2004), but 1000 years of Polynesian and European colonisation has resulted in the clearance of 85% of lowland native forest, predominantly for conversion to agricultural or production forestry lands (Collier 1992). This deforestation has resulted in the division of large continuous forest tracts into a network of smaller, isolated fragments (Franklin et al. 2002). The characteristics of these remnant forest fragments, such as their spatial arrangement, size, and degree of isolation, may determine the structure and functioning of local communities within the fragments (Barbosa & Marquet 2002; Hanski & Gaggiotti 2004).

The role of forest fragments in the maintenance of biodiversity, as a refuge for forest specialist species, and more specifically, the structural characteristics of forest fragments within habitat matrices, has received extensive attention in terrestrial ecosystems (Didham

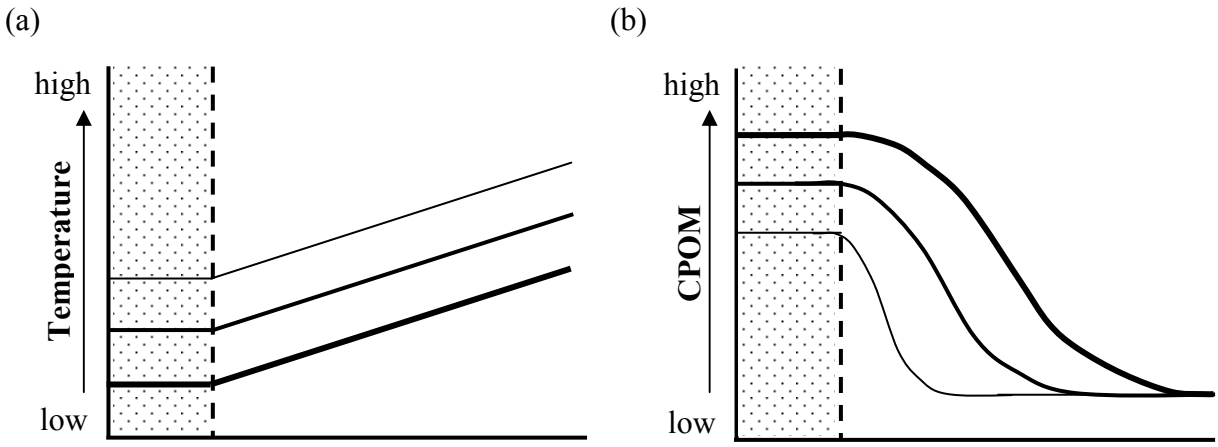
1997; Harrington et al. 2001; Ewers & Didham 2006a). Island Biogeography Theory, which focuses on population characteristics in response to the driving forces of fragment area and habitat isolation, has provided the conceptual foundation for much of this research (MacArthur & Wilson 1967). Island Biogeography Theory has been further developed through the investigation of edge and area effects, fragment shape, spatial and temporal isolation, and impacts of habitat connectivity on abiotic conditions and community structure (Didham 1997; Fahrig 2003; Lehtinen et al. 2003; Ewers & Didham 2006b). In contrast, the importance of forest fragment shape, isolation, connectivity, and particularly size has not been well studied in freshwater streams and rivers (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006).

Although many ecological concepts developed in terrestrial environments may be applicable to freshwaters, it is difficult to extrapolate their generalisations about forest fragmentation because of the unique nature of lotic ecosystems. Streams and rivers are dendritic networks embedded in a longitudinal continuum (Vannote 1980; Honnay et al. 2001; Campbell Grant et al. 2007) and therefore, upstream and downstream processes are dependent on the longitudinal and lateral connectivity of channels. For example, the unidirectional flow of streams and rivers results in terrestrial resources (i.e., leaf litter, woody debris and terrestrial invertebrates), deposited in forested upstream reaches, being transported downstream, thereby providing allochthonous energy subsidies to downstream reaches.

While the effect of forest fragmentation on streams and rivers is relatively unexplored, the significance of catchment vegetation in controlling stream ecosystem function is a fundamental theme in stream ecology (Fisher & Likens 1973; Vannote et al. 1980; Harding et al. 2006). In Chapter 2, I explored the effects of a forest–pasture gradient on stream environmental conditions and macroinvertebrate communities. Consistent with previous research (Harding & Winterbourn 1995; Quinn et al. 1997; Townsend et al. 1997; Benstead et al. 2003), I found that forested headwaters were characterised by high allochthonous inputs, low water temperatures, greater benthic diversity, and macroinvertebrate communities very different from those in open, pastoral stream reaches. An important focus for fragmentation research is applying this knowledge to developing riparian management techniques to restore and rehabilitate streams affected by vegetation removal and land use change. Considerable research has been undertaken to determine ideal riparian buffer widths and vegetation composition (Osbourne & Kovacic 1993; Quinn et al. 1993; Collier et al. 1995; Kiffney et al. 2004), however, the issue of how large a forest fragment needs to be to alter stream conditions sufficiently to support a benthic community

typical of a forest, has received little attention. Harding et al. (2006) drew attention to "forest reset effects", which have the potential to change a pastoral stream's condition, and therefore its biotic community, to that of a forested state, and to maintain this state for some distance downstream of the forest patch. However, the issue of how large a forest patch needs to be to have a reset effect continues to evade stream ecologists. In order to develop effective riparian management techniques, it is crucial that we gain an improved understanding of how riparian vegetation structure and size affect freshwater ecosystems.

In this chapter, I investigated how upstream forest fragment size influenced macroinvertebrate community composition in downstream pastoral reaches. Specifically, I determined the gradient of physico-chemical and biotic (both food resources and macroinvertebrate communities) change downstream from the forest, and whether these changes differed with increasing forest fragment size. Because large forests might have increased riparian shade, I predicted that the larger a forest fragment was, the lower a stream's temperature would be inside the forest, and that the rate of temperature increase would be the same downstream of forest fragments of all sizes (Fig. 3.1a). I also predicted that larger forest fragments would provide more detrital resources (e.g., terrestrially-derived coarse particulate organic matter) within the forest, than small forest fragments. Moreover, I expected that these detrital resources would be transported for greater distances downstream into pastoral reaches in streams flowing from larger rather than smaller forest fragments (Fig. 3.1b). These predictions were based on the assumption that large forest fragments would have a higher biomass of terrestrial resources available to supplement streams. Finally, if the above predictions held true, I further expected that macroinvertebrate species richness and "forest" benthic communities would respond to these forest subsidies, and be maintained further downstream in pastoral streams flowing from large than small forest fragments (Fig. 3.1c-d).



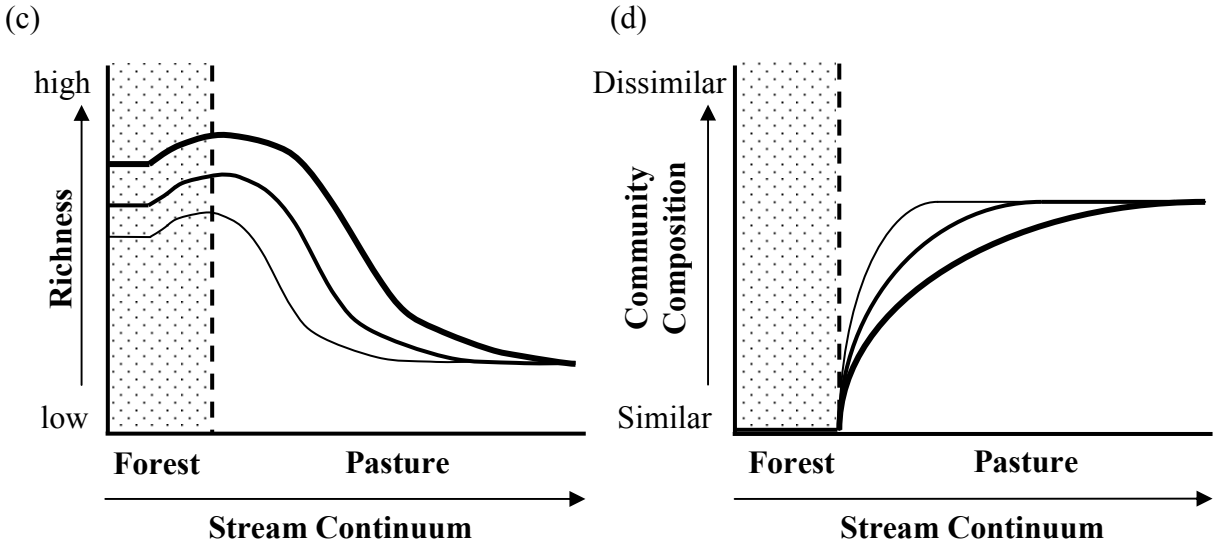


Figure 3.1 Conceptual model of the downstream effect of forest fragments of differing sizes on (a) physical variables (e.g., water temperature), (b) energy resources (e.g., CPOM), (c) macroinvertebrate richness, and (d) macroinvertebrate community composition in pastoral streams. Line thickness represents forest fragment size, where thin lines are small fragments, regular lines are medium fragments, and thick lines are large fragments.

3.2 Methods

3.2.1 Study sites

The study was conducted in eleven, first- and second-order streams in Canterbury, South Island, New Zealand. Canterbury incorporates several ecoregions, each classified by their own vegetative cover, bedrock geology, soils, relief and climate (Harding & Winterbourn 1997) (Table 3.1). Nine streams were located in High Country (HC) and one each in the lowland East Coast plains (EC) and Banks Peninsula (PE) ecoregions (Table 3.1). Of the nine streams located in the high country, four streams were in the Cass Basin (in or near Arthur's Pass National Park); three in the foot-hills near Mt. Nimrod, South Canterbury; one in the foot-hills of Alford Forest near Staveley; and one in the foot-hills west of Kaikoura. Of the two remaining sites, the East Coast plains stream was located south of Kaikoura, and the Banks Peninsula stream near Little River, south east of Christchurch (Fig. 3.2).

All streams in the Cass Basin were tributaries of the upper Waimakariri River. The headwaters of each stream originated in continuous native forest, dominated by mountain beech (*Nothofagus solandri* var. *cliffortioides*) with small isolated stands of red beech (*Nothofagus fusca*). The streams then flowed into open grassland, which consisted of a matrix

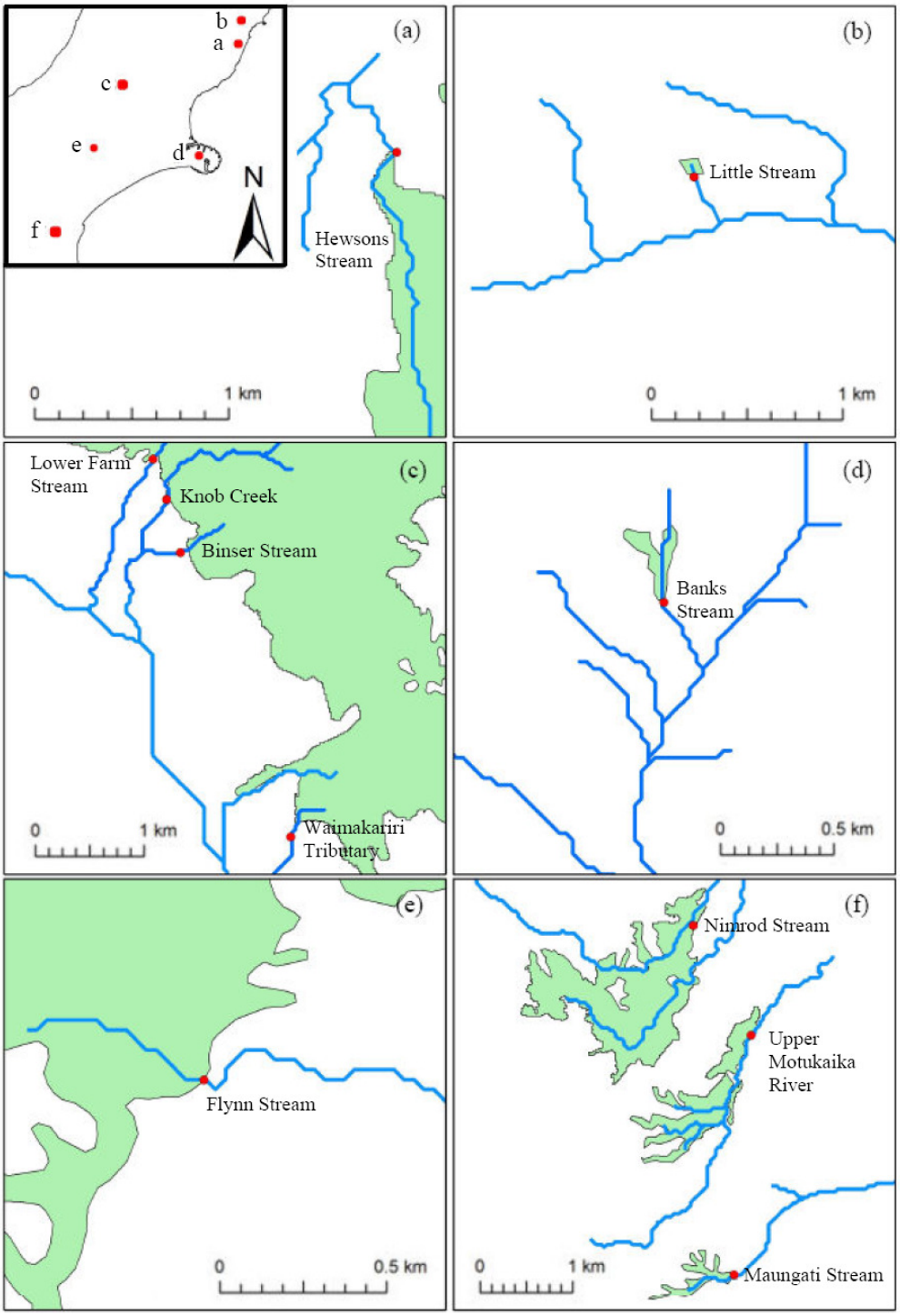


Figure 3.2 Eleven streams sampled throughout Canterbury (see inset) flowing from forest fragments (green areas) of different sizes into pasture (white areas). The six study areas were (a) south of Kaikoura; (b) inland of Kaikoura; (c) Cass Basin; (d) Banks Peninsula; (e) Alford Forest, Staveley; and (e) Mt. Nimrod, South Canterbury. The red symbols indicate the reach where physico-chemical and macroinvertebrate sampling was conducted nearby at 1 site upstream within the forest, and at 5-7 sites downstream of the forest, in pasture.

of mixed scrub, pasture and tussock species (*Chionochloa* spp.) grazed by sheep (Wardle 2002). The seven study streams located outside the Cass Basin also flowed from native forest fragments, dominated by broadleaf-podocarp forest, into pasture consisting predominantly of introduced grass species (e.g., ryegrass, white and red clovers) and moderately grazed by beef-cattle and/or sheep. Most eastern Canterbury lowland native forest fragments are remnants of a large broadleaf-podocarp forest dominated mainly by totara (*Podocarpus* spp.) along with rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), and kahikatea (*Dacrycarpus dacrydioides*) (Norton & Fuller 1994; Wardle 2002).

The eleven study streams differed in longitudinal slope and elevation, and flowed from forest fragments of different sizes (Table 3.2).

Table 3.1 The three South Island ecoregions and their characteristic climatic and geomorphological features used in the study. See Harding & Winterbourn (1997) for more complete ecoregion descriptions.

Ecoregion	Annual rainfall (mm)	Relief (m)	Vegetation	Soils	Geology
High Country (HC)	600-2400	300-2000	Tussock, grassland, scrub	Yellow-brown / grey earths	Greywacke, argillite
East Coast plains (EC)	400-1200	0-300	Improved grasses	Yellow-grey earths, recent	Glacial gravels
Banks Peninsula (PE)	1200-2400	300-1000	Grassland, scrub	Brown granular loams and clays	Volcanic basal flows

3.2.2 Survey design

All sampling was conducted in austral summer, between December 2008 and January 2009. Within each stream, multiple reach sites were sampled longitudinally both within and downstream of the forest fragment. The uppermost sampling site was located within the forest fragment, 25 m upstream of the forest-pasture edge (i.e., -25 m). A further five to seven reach sites were situated downstream within the pastoral land, along a $\log_{2.5}$ scale (i.e., 2.5, 6.3, 15.9, 38, 98, 256 and 612 m downstream of the forest fragment). Several streams were

sampled at maximum distances of 98 or 256 m from the forest fragment edge because they re-entered bush, dried up, or reached a confounding physical obstacle such as a culvert or dam (Table 3.2).

At each site, a range of in-stream physico-chemical parameters were measured. Dissolved oxygen (mg L^{-1} and percentage saturation; YSI 550A), temperature (ºC), pH and specific conductivity (μS_{25} cm^{-1}; OAKTON CON 10 series) were measured using standard meters. Specifically, temperature was measured at early to mid-morning, before peak noon and mid-afternoon temperatures. Stream channel characteristics, including average depth, width and substrate size, were also measured. Average channel depth was calculated from three evenly spaced measurements across the stream. Stream wetted width was measured across three representative channel widths within each sampling reach, and average substrate size was calculated by recording the length of the longest axis of 30 randomly selected particles.

Site location was recorded in the field using GPS (Garmin xTrexH GPS) and several catchment scale variables were calculated for each site from stream and catchment datasets (NIWA 2004) using GIS (ESRI ArcGIS 9.3). These included longitudinal stream slope and elevation using a 25 m digital elevation model (Table 3.2).

The benthic macroinvertebrate community was surveyed at each site by collecting three Surber samples (0.0625 m², 250 µm mesh) from a randomly selected riffle, and by taking a single composite kick-net sample (250 µm mesh) from a range of microhabitats within the study reach. Macroinvertebrate samples were preserved in the field in 70% ethanol.

Allochthonous inputs were estimated from ash-free dry weights (AFDW) of coarse particulate organic matter (CPOM; > 500 µm) collected within the replicate Surber samples. Biofilm was collected by taking five randomly selected medium or large cobbles (> 5 cm diameter) which were kept on ice and frozen upon returning to the laboratory for processing.

3.2.3 Macroinvertebrate, organic matter and biofilm processing

In the laboratory, Surber samples were sub-sampled due to extremely high macroinvertebrate densities. However, the entirety of each Surber sample was also scanned and any additional taxa not found in the sub-samples were added to the species lists, along with data from the kick-net samples. Each of the Surber sub-samples was rinsed thoroughly through a 250 µm mesh sieve to remove excess sediments and its contents were transferred to a Bogorov tray for counting and identification, under a low-powered (10x magnification) dissecting

Table 3.2 Locations and characteristics of the streams flowing from eleven forest fragments differing in size. Forest size class is defined as small (0-19.9 ha), medium (20-99.9 ha), and large (> 100 ha).

Stream name	Code	Ecoregion	Location	Total catchment area (ha)	Forest size in catchment (ha)	Forest size class	Elevation at forest edge (m)	Stream slope (degrees)	Stream order	Distance of most downstream site from forest edge (m)
Little Stream	S1	HC	Kaikoura	5.6	< 0.1	Small	320	8.9	1	98
Banks Stream	S2	PE	Banks Peninsula	58.7	7.6	Small	375	8.4	1	98
Maungati Stream	S3	HC	South Canterbury	58.5	12.0	Small	378	6.1	1	256
Knob Creek	M1	HC	Cass Basin	41.9	41.9	Medium	600	10.4	1	256
Flynn Stream	M2	HC	Alford Forest	64.4	48.9	Medium	489	7.4	1	98
Nimrod Stream	M3	HC	South Canterbury	62.8	58.1	Medium	318	10.4	2	256
Waimakariri Trib.	L1	HC	Cass Basin	386.8	201.4	Large	616	12.8	1	256
Hewsons Stream	L2	EC	Kaikoura	266.8	217.7	Large	79	5.6	1	256
Upper Motukaika River	L3	HC	South Canterbury	1268.4	227.3	Large	300	5.2	2	612
Binser Stream	L4	HC	Cass Basin	310.5	275.0	Large	557	12.1	2	612
Lower Farm	L5	HC	Cass Basin	555.9	413.8	Large	558	12.2	2	256

microscope (KYOWA model sdz-pl). Macroinvertebrates were identified to species, where possible (Towns & Peters 1996; Smith 2003; Winterbourn et al. 2006). However, many early instars or damaged specimens lacked the necessary physical features to key them to species, and these individuals were instead classified to genus or family.

All CPOM from the Surber samples was placed in foil weigh boats and dried, at 50ºC, for at least 48 h. Once dried, samples were ashed at 550ºC for 4 h and average AFDW (± 0.001 g) of CPOM was calculated for each site.

Biofilm biomass was measured using similar techniques. Frozen cobbles were thawed, a 0.021 m^2 quadrat was randomly placed on their exposed surfaces (facing upwards into the water column from the stream bed), and the area within each quadrat was scrubbed with a small wire brush. The scrubbed biofilm matter was rinsed into a container with filtered water, syringed through filter paper (Whatman® GF/C 47 mm, 1.2 µm pore size) and dried for at least 48 h at 50ºC. Once dried, samples were ashed at 550ºC for 4 h and average AFDW (± 0.001g) of biofilm was calculated for each site. The average AFDW of control filters was used to correct for mass lost by filters during the ashing process.

3.2.4 Statistical analyses

Prior to analyses, macroinvertebrates were grouped into taxonomic orders and functional feeding groups (shredders, scrapers, collector-browsers, predators, herb-piercers and filter-feeders) (Quinn et al. 2004; Mike Winterbourn pers. comm.). A measure of community evenness (or dominance) was calculated using the reciprocal of the Berger-Parker dominance index (Berger & Parker 1970):

$$1\text{-}D = N_{max} / N$$

where N_{max} is the number of individuals in the most abundant species and N is the total number of individuals collected. The Berger-Parker dominance index (1-D) can range from 0 to 1, where 1 indicates maximum evenness and 0 indicates complete dominance.

Linear mixed-effects (LME) models (using the *lme4* package in R, version 2.9.2.; R Development Core Team 2009) tested with maximum likelihood (ML) were used to explore the amount of variation in the response variables (stream physical, basal resource and macroinvertebrate variables) explained by the fixed covariate, distance from forest edge (m), and the fixed factor, forest size class in stream catchment (large, medium and small), while accounting for variation among the eleven study streams (random factor). To meet

requirements of normality and homogeneity of variances, average width, average depth, CPOM biomass, biofilm biomass, total macroinvertebrate density, EPT density, total macroinvertebrate richness, EPT richness, and axis 1 and 2 dissimilarity (see below) were log-transformed, whereas shredder density and scraper density were square-root transformed. Mixed-effects models were used because of the hierarchical design of the survey in which there was dependence of the distance effect upon different stream characteristics. I used model simplification to estimate *P* values and test the significance of the fixed effects distance, catchment forest size, and their interaction (Crawley 2007). Thus, predictors were removed one by one from the LME models and using ML, the Chi-square (χ^2) statistic and its significance level was estimated for each predictor and its interaction.

To establish overall macroinvertebrate community structure across distance gradients and forest fragments of different sizes, multivariate ordinations were performed in the statistical package CANOCO (version 4. 55; ter Braak & Smilauer 2006). An exploratory Detrended Correspondence Analysis (DCA) was performed on log-transformed macroinvertebrate abundance data to confirm that the longest gradient length (2.53) fell under the gradient threshold 3.0 (Leps & Smilauer 2003). This indicated that a Redundancy Analysis (RDA) was appropriate to analyse variability in macroinvertebrate community composition. Prior to performing the RDA ordination, I tested for collinearity among 10 environmental variables using a correlation matrix in STATISTICA (StatSoft, Inc. 2009). A paired correlation between dissolved oxygen percentage saturation (%) and dissolved oxygen concentration (mg L^{-1}) had an *r* value greater than 0.9, therefore dissolved oxygen concentration was excluded from the RDA ordination (Leps & Smilauer 2003). All other variables were used in the RDA. They were CPOM density, biofilm density, water temperature, channel width, average depth, average substrate size, pH, dissolved oxygen percentage saturation, and specific conductivity. The RDA explored macroinvertebrate community structure with the input of measured environmental stream predictors as driving forces. This analysis was performed on log-transformed macroinvertebrate abundances to down-weight the influence of rare taxa.

Finally, to test the effect of distance and catchment forest size on macroinvertebrate community composition, dissimilarity scores were calculated from the RDA axis scores (i.e., dissimilarity scores for both axis 1 and axis 2, separately) by subtracting each pastoral sample site axis score from its respective forest site (-25 m) axis score (c.f. Didham et al. 2009). This gave an indication of how different macroinvertebrate communities were downstream of the forest fragment. Finally, LME models were used to examine whether community

dissimilarity changed with downstream distance from the forest fragment, or with catchment forest size, and their interaction. As before, I used model simplification and ML to estimate *P* values and test the significance of distance, catchment forest size, and their interaction.

3.3 Results

3.3.1 Physico-chemical, basal resource and macroinvertebrate change

A mixed effects model showed that water temperature significantly increased with increasing distance downstream of the forest fragment (Fig. 3.3a, Table 3.3). There was also a significant interaction effect, indicating that temperature increased more slowly with distance downstream in streams that flowed through larger forest fragments than streams flowing through small- and medium-sized forest fragments (Fig. 3.3a, Table 3.3). For example, water temperature increased by 3.9 ºC and 4.2 ºC after 256 m in streams flowing through small and medium forest fragments, respectively, but only increased by 3.3 ºC after 612 m in streams flowing through large forest fragments. Average substrate size, depth and width showed no significant change with distance from the forest fragment, and was not affected by upstream forest fragment size (Fig. 3.3b-d, Table 3.3).

Mixed effects models of in-stream basal resources showed that CPOM biomass was greatest within forest fragments but decreased with increasing distance downstream into pasture (Fig. 3.4a, Table 3.3). On average, CPOM biomass decreased by 43% (from 99 g per m² in the forest to 56 g per m²) in the first 2.5 m downstream of the forest fragment. From 2.5 m to 256 m below the forest, CPOM biomass declined less rapidly to 49 g per m². In streams flowing through large forest fragments, CPOM biomass declined as much as 75% by 612 m into pasture, however, there was no clear evidence to suggest that forest size influenced the amount of CPOM being transported downstream. Thus, there was no significant difference in the rate of decline in CPOM biomass in streams flowing from different sized forest fragments (Fig. 3.4a, Table 3.3). Biofilm biomass did not change significantly with longitudinal distance downstream from the forest fragment, or with increasing forest fragment size (Fig. 3.4b, Table 3.3).

A total of 85 taxa was collected from 73 sites (Appendix 2). Different measures of macroinvertebrate taxa richness and abundance responded in different ways to stream distance and forest fragment size (Fig. 3.5, Table 3.4). Total taxonomic richness decreased significantly with increasing distance downstream from the forest fragment (Fig. 3.5a, Table 3.4). In forest there was an average of 27 taxa, but this fell to 25 and 17 taxa, repectively at

256 m and 612 m downstream in pasture. Similarly, EPT richness declined significantly from an average of 13 taxa within the forest, to 8 taxa 612 m downstream of the forest (Fig. 3.5c, Table 3.4). However, both total taxonomic and EPT richness showed no response to increasing forest fragment size (Table 3.4). In contrast, distance-forest size interactions affected both EPT and scraper densities (Fig. 3.5d & f, Table 3.4). EPT density did not appear to change between forest and pasture in streams flowing from large forest fragments.

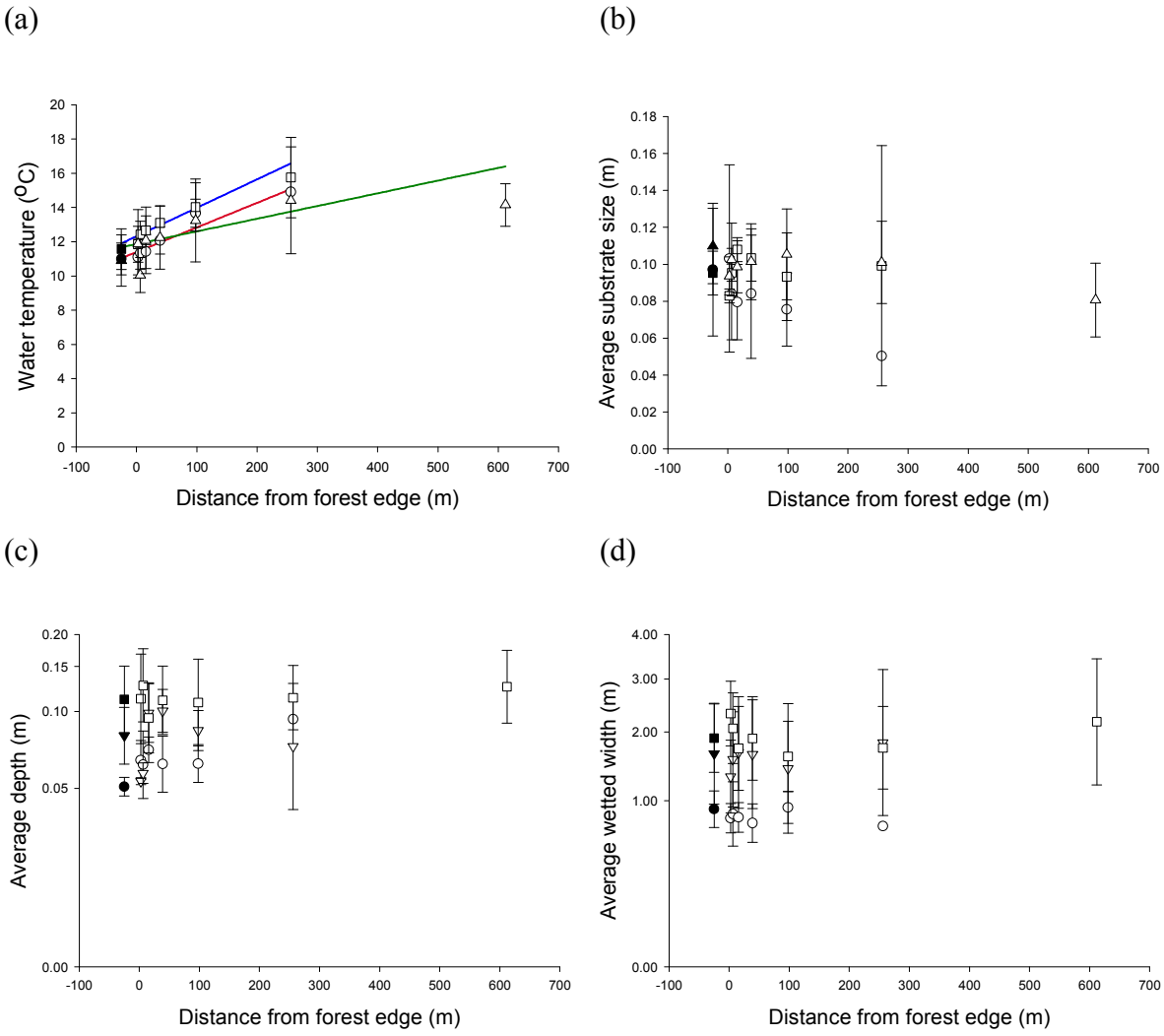


Figure 3.3 Mean (± 1 SE) (a) water temperature, (b) substrate size, (c) stream depth, and (d) wetted width in streams flowing through small (n = 3, circles), medium (n = 3, squares) and large (n = 5, triangles) forest fragments into pasture up to 700 m downstream. Solid symbols are forested sites and open symbols are pasture sites. Green (large forest), blue (medium forest) and red (small forest) lines indicate significant distance and forest size interaction effects.

Table 3.3 Mixed effects model outputs for physical and biotic parameters in streams flowing from small (0–19.9 ha), medium (20–99.9 ha) and large (> 100 ha) forest fragments. *P* values in bold indicate significant differences at α = 0.05.

Response	Effect variable	Variance	d.f.	X^2	*P*
Temperature (ºC)	Stream (random)	11.96			
	Distance		1	42.52	**< 0.001**
	Forest size		2	0.25	0.883
	Distance x Forest size		2	8.68	**0.013**
Average substrate size (m)	Stream (random)	< 0.01			
	Distance		1	2.06	0.152
	Forest size		2	0.34	0.845
	Distance x Forest size		2	0.64	0.725
Average sample site depth (m)	Stream (random)	0.30			
	Distance		1	0.08	0.775
	Forest size		2	3.13	0.209
	Distance x Forest size		2	2.23	0.328
Average wetted width (m)	Stream (random)	0.50			
	Distance		1	3.44	0.064
	Forest size		2	2.30	0.317
	Distance x Forest size		2	0.28	0.872
CPOM biomass (g/m²)	Stream (random)	0.09			
	Distance		1	4.17	**0.041**
	Forest size		2	2.59	0.274
	Distance x Forest size		2	2.51	0.286
Biofilm biomass (g/m²)	Stream (random)	0.13			
	Distance		1	0.06	0.803
	Forest size		2	3.12	0.210
	Distance x Forest size		2	4.60	0.100

However, in streams flowing through medium-sized forest fragments, EPT density increased from an average of 6,700 individuals per m² in the forest to 7,500 individuals per m² 256 m downstream in pasture. Streams flowing through small forest fragments showed the opposite effect, with densities decreasing rapidly from 5,700 individuals to 1,800.

Scrapers (primarily *Potamopyrgus* spp.) showed more rapid increases in density with decreasing forest fragment size (Fig. 3.5f). Although scraper densities in streams flowing from large forest fragments remained relatively low along the entire studied length (e.g., 130 per m² in forest increased to 180 per m² 256 m below forest), streams from medium and small

fragments showed increases in density (420 per m² in forest to 970 per m² 256 m below forest, and 1,180 per m² in forest to 21,800 per m² 256 m below forest, respectively). On the other hand, there was no evidence to suggest that total macroinvertebrate density or shredder density (e.g., *Acroperla trivacuata, Austroperla cyrene* and *Triplectides* spp.) changed significantly with longitudinal distance downstream from the forest fragment, or with increasing forest fragment size (Fig. 3.5b & e, Table 3.4).

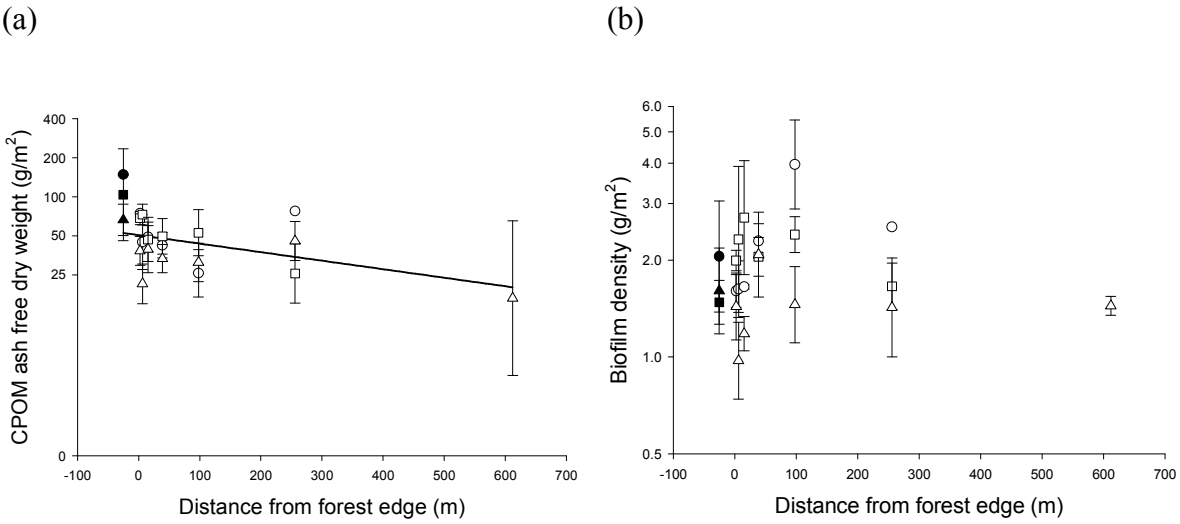
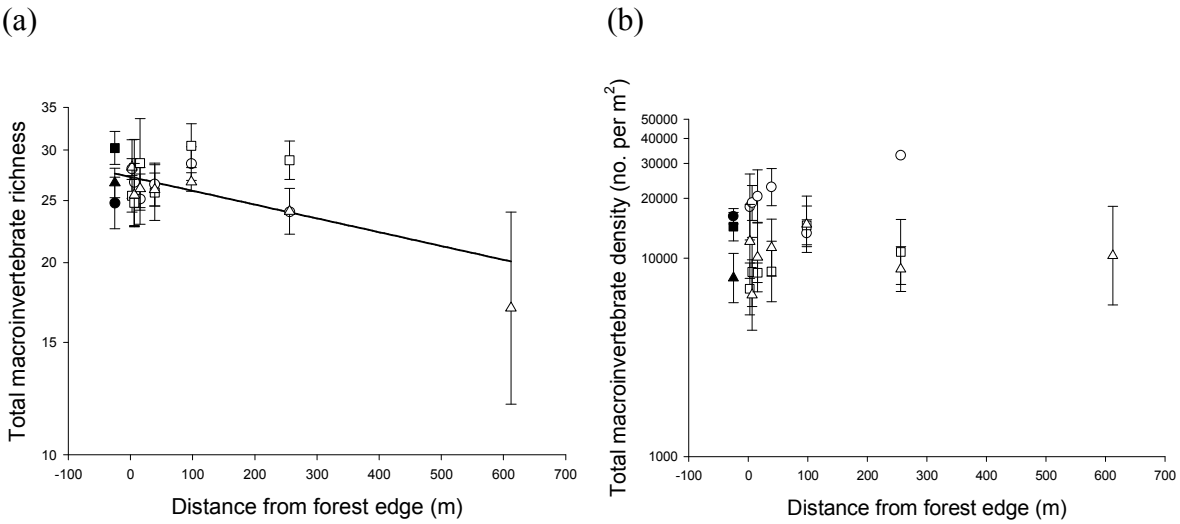


Figure 3.4 Mean (± 1 SE) (a) CPOM biomass, and (b) biofilm biomass in streams flowing through small (*n* = 3, circles), medium (*n* = 3, squares) and large (*n* = 5, triangles) forest fragments into pasture 700 m downstream. Solid symbols are forested sites and open symbols are pasture sites. Where appropriate a solid line indicates a significant distance effect among all forest sizes.



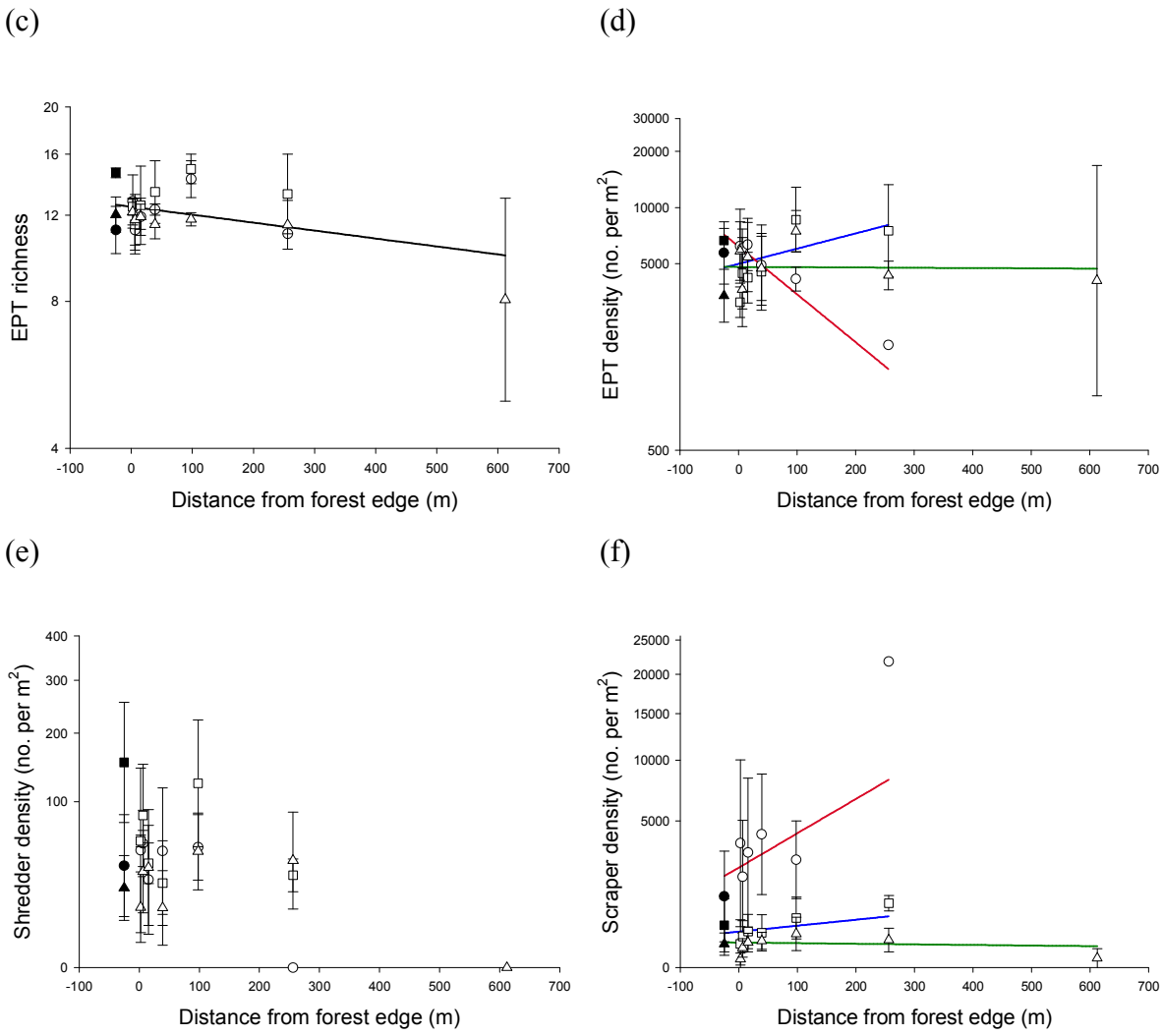


Figure 3.5 Mean (± 1 SE) (a) total taxonomic richness, (b) macroinvertebrate density, (c) EPT richness, (d) EPT density, (e) shredder density, and (f) scraper density in streams flowing through small (n = 3, circles), medium (n = 3, squares) and large (n = 5, triangles) forest fragments into pasture 700 m downstream. Solid symbols are forested sites and open symbols are pasture sites. Where appropriate a solid black line indicates a significant distance effect among all forest sizes. Green (large forest), blue (medium forest) and red (small forest) lines indicate significant distance and forest size interaction effects.

The Berger-Parker dominance index (1-D) indicated that streams flowing through large- and medium-sized forest fragments were characterised by communities with low dominance, compared with small-sized forest fragments (Fig. 3.6, Table 3.4). Community dominance increased with increasing distance downstream of the forest fragment in streams flowing from forest fragments of all sizes, however, there was no distance-forest size

interaction effect. That is, macroinvertebrate communities in streams flowing from small forest fragments were more strongly dominated by individual taxa along the entire stream continuum, but the rate at which dominance increased downstream of the forest was no different than in streams flowing from medium- and large-sized forest fragments.

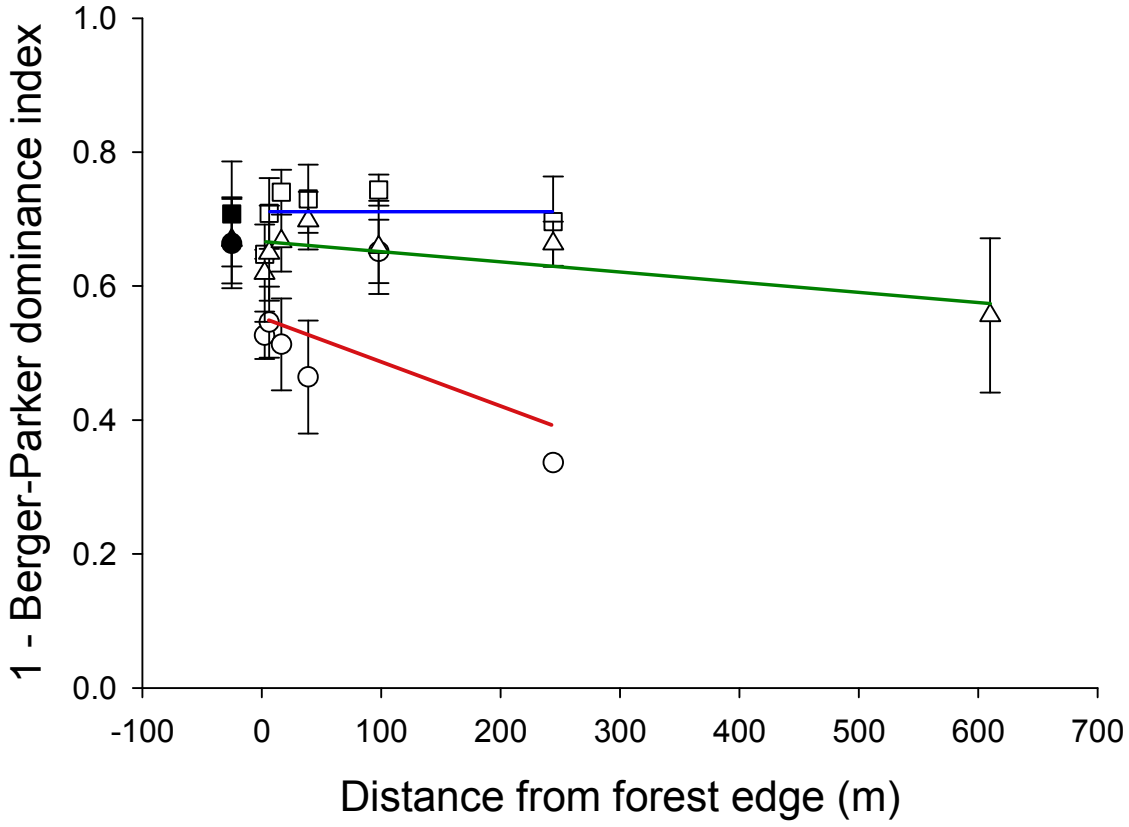


Figure 3.6 Mean (± 1 SE) reciprocal Berger-Parker index in streams flowing through small (n = 3, circles), medium (n = 3, squares) and large (n = 5, triangles) forest fragments into pasture up to 612 m downstream. Solid symbols are forested sites and open symbols are pasture sites. Green (large forest), blue (medium forest) and red (small forest) lines indicate a significant distance and forest fragment size effect.

3.3.2 Environmental variables driving downstream changes in communities

An RDA ordination was used to test overall macroinvertebrate community structure in relation to distance from the forest edge and forest size (Fig. 3.7). Axis 1 explained 16.4% of the variation in species composition and 57.9% of the species-environment relationship variation. The order of communities along axis 1 was primarily a function of stream width and depth. Temperature and substrate size were also partially correlated with axis 1 but were

more highly associated with community structure along axis 2. Axis 2 explained a further 7.4% variation in the species data and 26.3% variation in the species-environment relationship.

Community dissimilarity, calculated from RDA ordination axis 1, showed no change with increasing distance below forest fragments in pasture or with increases in upstream forest fragment size (Fig. 3.8a, Table 3.5). In contrast, community structure, along ordination axis 2, became significantly different in pasture sites with increasing distance downstream from the forest edge (Fig. 3.8b, Table 3.5). Specifically, overall macroinvertebrate community composition changed rapidly from that in forest with increasing distance in pasture. However, upstream forest size had no effect on the gradient of community structure change downstream (Table 3.5). Temperature seems to have been the primary driver of community dissimilarity (Fig. 3.7).

Table 3.4 Mixed effects model outputs for macroinvertebrate response parameters and indices in streams flowing from small (0–19.9 ha), medium (20–99.9 ha) and large (> 100 ha) forest fragments into pasture. *P* values in bold indicate significant differences at α = 0.05.

Response	Effect variable	Variance	d.f.	χ^2	*P*
Total macroinvertebrate richness	Stream (random)	0.01			
	Distance		1	11.40	**< 0.001**
	Forest size		2	0.82	0.662
	Distance x Forest size		2	5.62	0.060
Total macroinvertebrate density (individuals per m²)	Stream (random)	0.26			
	Distance		1	1.11	0.292
	Forest size		2	3.20	0.202
	Distance x Forest size		2	0.06	0.973
EPT richness	Stream (random)	0.01			
	Distance		1	4.45	**0.033**
	Forest size		2	2.25	0.325
	Distance x Forest size		2	3.65	0.161
EPT density (individuals per m²)	Stream (random)	0.35			
	Distance		1	0.22	0.643
	Forest size		2	0.10	0.953
	Distance x Forest size		2	13.20	**0.001**
Shredder density (individuals per m^2)	Stream (random)	17.00			
	Distance		1	3.59	0.058
	Forest size		2	1.15	0.563

	Distance x Forest size		2	3.67	0.159
Scraper density (individuals per m^2)	Stream (random)	685.95			
	Distance		1	1.09	0.298
	Forest size		2	4.93	0.085
	Distance x Forest size		2	14.49	**< 0.001**
Berger-Parker index (1-D)	Stream (random)	< 0.01			
	Distance		1	4.14	**0.042**
	Forest size		2	7.40	**0.025**
	Distance x Forest size		2	1.87	0.392

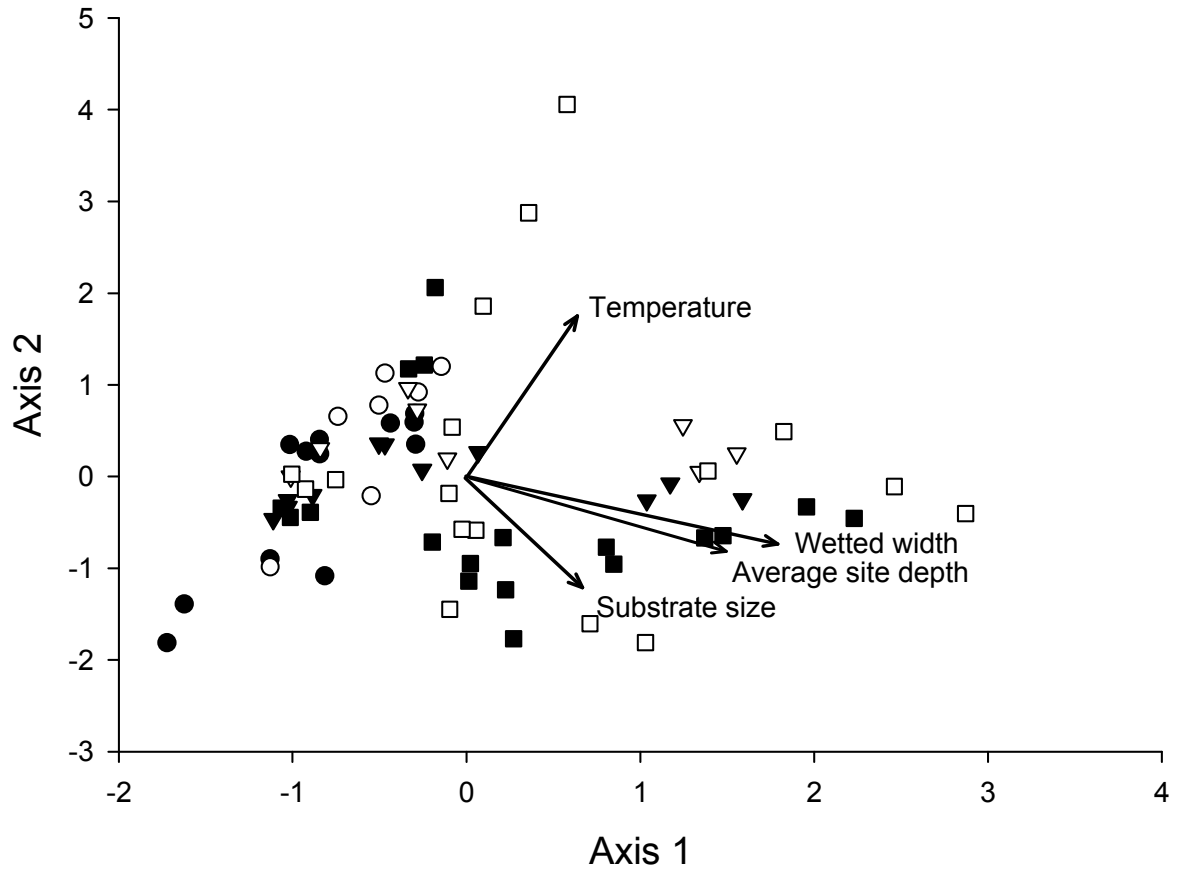


Figure 3.7 A redundancy analysis (RDA) ordination of macroinvertebrate communities and associated significantly correlated environmental data collected at all sites. Solid symbols are forest sites and open symbols are pasture sites below small (n = 3, circles), medium (n = 3, squares) and large (n = 5, triangles) forest fragments.

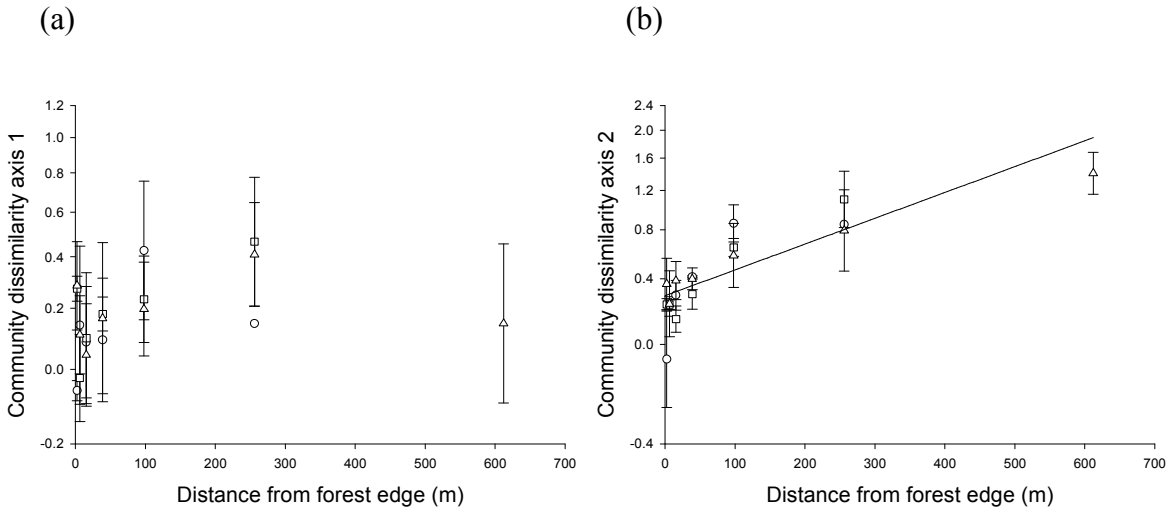


Figure 3.8 Mean (± 1 SE) community dissimilarity along (a) RDA ordination axis 1, and (b) axis 2 in streams flowing through small (n = 3, circles), medium (n = 3, squares) and large (n = 5, triangles) forest fragments into pasture 700 m downstream. Solid symbols are forested sites and open symbols are pasture sites. Where appropriate a solid line indicates a significant distance effect among all forest sizes

Table 3.5 Mixed effect model outputs for community dissimilarity response parameters in streams flowing from small (0–19.9 ha), medium (20–99.9 ha) and large (> 100 ha) forest fragments into pasture. P values in bold indicate significant differences at $\alpha = 0.05$.

Response	Effect variable	Variance	d.f.	χ^2	P
Dissimilarity axis 1	Stream (random)	0.04			
	Distance		1	1.91	0.167
	Forest size		2	0.04	0.982
	Distance x Forest size		2	2.46	0.293
Dissimilarity axis 2	Stream (random)	0.01			
	Distance		1	22.20	**< 0.001**
	Forest size		2	0.30	0.861
	Distance x Forest size		2	5.76	0.056

3.4 Discussion

Physical, biotic, and macroinvertebrate parameters of streams changed downstream of forest fragments in a manner consistent with my initial predictions. In particular, water temperature increased, and CPOM biomass and macroinvertebrate richness decreased, with increasing distance downstream of forest fragments across all streams. This finding is consistent with the results of previous research into the longitudinal recovery of pastoral streams when they enter forest, in which temperature decreased, and benthic community metrics changed, with increasing distance into the forest (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006). In contrast, few studies have looked at changes in water temperature, CPOM biomass, or macroinvertebrates along a longitudinal stream gradient from forest to pasture (c.f. Chapter 2).

3.4.1 Does the size of a forest fragment affect stream physical conditions?

The effect of forest fragment size on the response of stream environmental conditions, such as water temperature, has been poorly studied. Exceptions are Rutherford et al. (1997) and Davies-Colley (1997) who showed that temperature was strongly affected by stream width, which was influenced by the height and canopy structure of streamside vegetation. I predicted that larger forest fragments would maintain lower stream temperatures within forested reaches but as the stream flowed into the open, uniform rates of increase below fragment edges would occur. Contrary to my expectations, results showed that stream temperature did not differ within forest fragments greater than 7 ha in size, and that streams flowing downstream from large fragments increased in temperature less rapidly than those flowing from small- and medium-sized fragments. As a result, the magnitude of temperature increase was approximately 4ºC 250 m below small and medium- sized forest fragments, significantly greater than the 3.3ºC increase shown over 612 m below large fragments.

The fact that stream temperature was the same at forested sites in forest fragments of all sizes suggests that canopy shading is generally similar in forest fragments greater than 7 ha in size. New Zealand studies have largely neglected the effect of patch size on stream temperature but some international research has looked at the impacts of buffer width. For example, Nakamura & Yamada (2005) examined the effects of pasture development on the ecological functions of riparian forests in Northern Japan and suggested that a riparian buffer width of 15-20 m should be preserved to maintain sufficient shading of a stream. Others have suggested widths of 30 m in the western U.S. (Brazier & Brown 1973; Spence et al. 1996),

and 10-20 m in the eastern U.S. (Aubertin & Patric 1974). Some New Zealand native forest provides strong shading of small streams, and light exposure has been found to decrease abruptly from that exhibited in pasture by only 10 m inside a forest's edge (Davies-Colley et al. 2000). This suggests that relatively small fragments, similar to those found in my survey (averaging 7 ha in size), are able to maintain cool water temperatures similar to those of larger forest fragments.

Why a stream flowing below a small or medium-sized forest fragment could increase in temperature more rapidly in pasture than one flowing below a large fragment is far less obvious. This is because the size of a forest upstream should have no climatic affect on solar and atmospheric radiation inputs into a stream below the forest edge. Logically, heating of larger streams requires greater solar radiation than smaller streams. Other studies have shown stream width to narrow in pasture downstream from forest (Davies-Colley 1997; Trimble 1997), which in turn would be expected to offset some of the potential temperature increases downstream than if stream width remained the same. However, my study streams showed no difference in width or depth between forest and pasture, and more specifically, streams flowing from large forest fragments did not narrow more abruptly in pasture than streams flowing from medium- and small-sized forest fragments.

The likely explanation for the more rapid increase in temperature below medium and small forest fragments is probably due to location differences between sample sites. Although streams were located in similar ecoregions (9 out of 11 in High Country; Table 3.2), each stream's subregion (or sub-ecoregion as termed by Harding & Winterbourn (1997)) would have likely impacted stream condition. Thus, the majority of sampled streams that flowed through large forest fragments (3 out of 5) were located in the montane environment of the Cass Basin, whereas most streams flowing through medium (2 out of 3) and small (3 out of 3) forest fragments were in foothill environments. Compared to their foothill counter-parts, streams in the montane environment would have been subjected to lower air temperatures, less intensive solar radiation, higher rainfall, and different pasture grasses upon entering open landscapes downstream of the forest. These factors would have contributed to thermal energy variation and by implication a slower increase in water temperature downstream of forest fragments.

3.4.2 Does the size of a forest fragment affect stream allochthonous and autochthonous resources?

The amounts of downstream allochthonous and autochthonous stream resources were expected to be markedly affected by upstream forest fragment size. In Chapter 2, I established that the subsidy of organic material from continuous forest had been lost by approximately 300 m downstream from the forest edge in Mt. Taranaki headwater streams. Results in this study showed, that in Canterbury headwater streams, the reduction in organic matter occurred more slowly, from an average 50 g per m^2 to 35-40 g per m^2 of in-stream organic matter over 300 m. Unlike Mt. Taranaki sites (c.f. Chapter 2), CPOM was also exported at appreciable levels (greater than 20 g per m^2) for at least 600 m downstream from the forest. I predicted that forest fragment size would have a fuelling effect on the nature of this relationship, as larger forest fragments were anticipated to subsidise and maintain higher amounts of detritus in downstream pasture sites farther downstream than medium and small sized forest fragments. Instead, allochthonous subsidies appeared to be similar downstream of all forest fragments regardless of size. Streambed retention probably had a significant impact on this downstream export of allochthonous resources. This means that streams flowing from small forest fragments may have been better equipped to retain the small amounts of organic matter they supplied streams in forest than streams from medium and large fragments, which may have had low retention and therefore much of their organic matter was simply flushed downstream out of the system. Alternatively, small- and large-sized forest fragments may have simply had similar CPOM inputs into stream channels.

I expected biofilm to increase downstream in the pasture reaches, due to greater light levels than in shaded forest. In a study of agriculture stream recovery in Waikato, New Zealand, Scarsbrook & Halliday (1999) found epilithon biomass decreased upon flowing into native forest. In contrast, my results showed that biofilm biomass did not differ at increasing distances below forest. This finding was consistent with that obtained in Mt. Taranaki streams where no change in chlorophyll-*a* biomass was observed between continuous forest and pasture (c.f. Chapter 2). Biofilm biomass also showed no change in relation to forest fragment size. An absence of biofilm differences between forest and pasture may have been the result of disturbance events, such as high flows, coupled with unstable substrates and macroinvertebrate grazing removing and preventing expected periphyton growth (Biggs & Close 1989; Biggs 2000; Cardinale et al. 2006). Biggs et al. (1999) found that flood flows and bed movement greatly reduced periphyton biomass in South Island headwater streams. Also, Harding & Winterbourn (1995) found no difference in periphyton biomass in forest

versus pasture streams in Canterbury. They suggested that low periphyton biomass in pastoral streams may have resulted from shading of substrates by dense grasses, or that livestock disturbance may have reduced water clarity, increased sedimentation, and decreased substrate stability.

3.4.3 Macroinvertebrate community responses to forest fragmentation

Considerable decreases in total taxonomic and EPT richness were evident with increasing distance downstream but were unrelated to upstream forest size. This contrasts with earlier predictions that anticipated taxonomic richness would decline downstream of forest more rapidly with increasing upstream forest size. Scarsbrook & Halliday (1999) found a similar effect where total macroinvertebrate and EPT richness increased in streams flowing from pasture into patches of late successional indigenous riparian forest in the Waikato. They showed that within 300 m of entering forest, EPT richness had increased significantly. On the other hand, Storey & Cowley (1997) showed that the taxonomic richness of a stream initially in pasture increased 600 m inside a forest northwest of Auckland. Storey & Cowley (1997) and Scarsbrook & Halliday (1999) provide compelling evidence that in addition to measures of buffer width and forest patch size, the shape and therefore the length of forest covering a stream channel is important for determining community structure.

Total macroinvertebrate density was expected to increase in pasture following a large increase in the density of scrapers, particularly molluscs. However, total macroinvertebrate density remained unchanged downstream and did not differ between streams flowing from different forest sizes. Likewise, forest fragment size and distance downstream had no effect on shredder density, which was surprising as shredder density was expected to follow longitudinal decreases in CPOM biomass. These findings were in stark contrast to findings obtained from Mt. Taranaki streams where total macroinvertebrate densities increased downstream in response to increases in the number of scrapers, and shredder density decreased sharply coinciding with drops in CPOM (c.f. Chapter 2). Indeed, increased macroinvertebrate densities in pasture compared to forest within a catchment have been found elsewhere (Scarsbrook & Halliday 1999; Niyogi et al. 2007). However, Scarsbrook & Halliday (1999) suggested that this was due to water quality, whereas Niyogi et al. (2007) found that fine sediments on stream bed substrata had a large impact on invertebrate indices.

In-stream EPT and scraper densities responded to a change in forest fragment size at study sites, but trends were inconsistent. EPT and scraper densities remained unchanged between stream sites in and downstream of large forest fragments. On the other hand, streams

flowing from medium-sized forest fragments showed increases in scraper and EPT densities, whereas streams flowing from small forest fragments showed an even faster increase in scrapers, but a decrease in EPT numbers downstream. The reasons for these patterns are unclear, however, the Berger-Parker dominance index (1-D) indicated that single taxa dominance increased downstream. That is, EPT density may have dropped severely due to increased community dominance and competition from abundant scrapers, predominantly molluscs, in streams flowing from small forest fragments. In contrast, scraper densities in streams flowing downstream of medium and large fragments did not increase as severely and potentially did not out-compete EPT communities.

Expanding on these results, I expected that overall community structure would become progressively different downstream of forest fragments, and that the change would occur most rapidly downstream of smaller forest fragments. Primarily, this prediction was made based on the expectation that resource subsidies would be more abundant at stream sites below large rather than medium and small forest fragments. Dissimilarity scores, obtained from an RDA ordination of taxa densities, indicated that decreasing temperature primarily drove significant changes in macroinvertebrate community structure downstream (i.e. RDA axis 2). This was contrary to observed community dissimilarity in Mt. Taranaki streams, which indicated that pasture communities became increasingly different from forest communities with increasing distance below forest associated with changes in CPOM biomass (c.f. Chapter 2, RDA axis 1). The Berger-Parker index (1-D) supports this evidence as it showed that communities in pasture reaches were more highly dominated by single species populations than those in forest where taxa were more evenly represented. Additionally, communities were more highly dominated at all sites (in forest and pasture) in streams flowing from small forest fragments than the more even communities in streams flowing from medium and large forest fragments. However, dissimilarity analyses showed no effect of forest fragment size on community structure. The longitudinal study on the recovery of three small second order pastoral streams in the Kaipara region of Northland, found aquatic invertebrate communities changed between pasture and forest (Storey & Cowley 1997). Storey & Cowley (1997) found that benthic macroinvertebrate communities shifted from a more enrichment-tolerant to a more clean-water fauna within 600 m of re-entering native forest remnants. No studies, to my knowledge, have examined community change over a longitudinal forest-pasture land-use gradient and related the results to forest size.

3.4.4 Managing riparian vegetation to maintain forest macroinvertebrate communities

In New Zealand, rural land-uses are perceived to be the primary cause of degradation of streams and rivers (Smith 1993). A practical solution for rehabilitating and restoring streams and rivers from the effects of agriculture is to plant riparian forest along stream banks. Forested riparian areas in open landscapes can aid in the maintenance of stream diversity (Heartsill-Scalley & Aide 2003). Some studies have shown recovery of both water quality and benthic communities of agricultural streams when entering forest remnants. For example, Storey & Cowley (1997) showed that temperature had returned to forest-stream levels 300 m into the forest, and the fauna had became similar to that of a forested control stream in terms of taxonomic richness and Macroinvertebrate Community Index (MCI) by 600 m in three Northland streams. Scarsbrook & Halliday (1999) also found that aquatic invertebrate community composition of three first-order pastoral streams in the Waikato showed shifts towards native forest condition just 50 m into the forest remnants, and full recovery within 300 m. In contrast to these two studies, Harding et al. (2006), in a study of the ability of forest fragments to mitigate the adverse effects of agriculture on water quality and aquatic species, showed partial recovery, but found that the forest fragments investigated were not of sufficient length to return streams to forest conditions. This finding raised the question, "how big does a forest fragment need to be to sufficiently mitigate the adverse effects of agricultural land-uses?" Frequently, financial and land ownership issues conflict with the abilities of resource managers to replant entire stream reaches. Thus, developing a sound understanding of how riparian size affects stream condition and biota is important in mitigating agricultural impacts.

I have shown that upstream forest size can significantly affect a stream's abiotic and biotic conditions, including downstream macroinvertebrate community structure. My results indicate the potential impact that replanting forest patches of different sizes could have on downstream trends following a "forest reset effect" (Harding et al. 2006). However, establishing precise rules based on the rate and magnitude of downstream changes in relation to upstream forest size has proven to be difficult. Having said that, my results do suggest some important trends. Firstly, relatively large forest fragments (> 100 ha) may be required to maintain cool summer water temperatures for considerable distances downstream in pastoral reaches. Secondly, small forest fragments (< 7 ha) may supply moderate to high organic resources, similar to that of larger forest fragments, to streams, which are essential basal food resources for many forest taxa. Finally, there is some evidence to suggest that larger forest patches may benefit communities both within forest and downstream in pasture, particularly

in terms of reducing community dominance by molluscs. However, some studies (e.g., Storey & Cowley 1997; Scarsbrook & Halliday 1999; Nakamura & Yamada 2005) suggest that both forest buffer length and buffer width along a stream continuum are important factors in maintaining in-stream forest taxa. Therefore, forest patch shape, including measures of both width and length, should be included in future riparian management studies.

The ability to establish strong relationships in this study was hindered by the innate complexity of stream ecosystems and their interactions with surrounding land-uses. In order to truly investigate the nature of stream macroinvertebrate community change relative to riparian forest size, it is essential to also measure forest fragment shape, length, and isolation, and incorporate theory based on habitat edge effects (Ewers & Didham 2006b). Furthermore, the composition and nature of riparian buffers have significant implications for the ecology of streams. Height, density and proximity of riparian vegetation relative to streams have implications for driving water channel thermal regimes (Poole & Berman 2001), which could have residual effects on community responses. Despite the likely importance of all these factors, studies on the effects of fragmentation on terrestrial species have shown that fragment size can be a crucial first measure in testing the impacts of habitat fragmentation by deforestation (Harding et al. 2006). Resource managers require a framework based on experimental data in order to employ sufficient riparian management techniques to mitigate and restore the adverse effects of agriculture on streams. Therefore, the challenge for freshwater ecologists is to assess the quantifiable responses of stream communities to the physical characteristics and sizes of forest fragments. An appropriate step for understanding what physical forest/riparian mechanisms are responsible for the maintenance of stream communities would be to mimic riparian buffers through manipulating and isolating key drivers, such as detrital resources or temperature regimes.

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Chapter 4: Can the addition of organic matter modify pastoral stream macroinvertebrate communities?

4.1 Introduction

The importance of surrounding land-use on stream ecosystems is a fundamental concept in stream ecology (Hynes 1975; Vannote et al. 1980; Wallace et al. 1997). Forested streams typically have cool, clear water with low nutrient enrichment, high habitat heterogeneity, abundant allochthonous resources (i.e., terrestrial leaf litter, wood and invertebrates), and diverse in-stream communities, including some forest specialists (Collier et al. 1995; Harding & Winterbourn 1995; Quinn et al. 1997). However, over the past approximately 900 years, New Zealand experienced a widespread conversion of forest, mostly to agriculture, that cleared 85% of the country's once dense, native lowland forest (Collier 1992). Deforestation resulted in a proliferation of open, pastoral streams that became degraded and impacted by anthropogenic disturbances. The pastoral intensification of streams usually results in high summer temperatures, poor water quality, low habitat heterogeneity, abundant autochthonous resources (i.e., algae and macrophytes), and less diverse benthic communities dominated by generalists (Collier et al. 1995; Harding & Winterbourn 1995; Quinn et al. 1997). Changes from forested to pastoral stream conditions occur rapidly along stream continua (see Chapters 2 & 3).

The replanting of pastoral stream banks has been a common approach to mitigate the adverse effects of agriculture. Nevertheless, it is often both financially and logistically difficult to surrender pastoral land for riparian use. One of the challenges for stream ecologists is to provide alternative strategies that might mitigate the negative impacts that increases in agricultural intensity have had on stream water quality, habitat, and biotic communities. Scarsbrook & Halliday (1999) suggested that planting patches of riparian vegetation along a pastoral stream might restore in-stream conditions to those of a forested stream. In fact, there has been much work investigating the recovery of modified stream communities passing through agricultural land use and entering forest patches (e.g., Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006). For example, Harding et al. (2006) suggested that a "forest reset effect" might occur when a forest fragment is large enough to have a positive effect on the physical and chemical conditions of a stream, not only within the forest, but also for some distance downstream into pasture. The improved

conditions might include altered temperature regimes with lower summer highs and more moderate winter lows, reduced sedimentation and turbidity, shifts in stream resources from typically autochthonous production to allochthonous inputs, and more diverse macroinvertebrate communities (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006; Niyogi et al. 2007). Understanding how a forest fragment might maintain in-stream biodiversity could provide important insights into how to best manage and conserve freshwater ecosystems. Through knowledge of the key abiotic and biotic conditions to which freshwater biota respond, resource managers may focus on restoring riparian characteristics that maximise such conditions and therefore have a high potential to reset and restore pastoral streams to a forested state comparable to that found before human settlement of New Zealand.

Benstead et al. (2003) suggested that shifts in the invertebrate communities of low-order streams affected by deforestation are driven principally by biotic processes controlled by riparian vegetation. Re-establishing riparian zones can reduce primary production and increase inputs of terrestrial carbon (e.g. Scarsbrook & Halliday 1999). In particular, terrestrial vegetation that enters a stream channel provides an important source of detrital food and habitat for many stream organisms (Kaushik & Hynes 1971; Allan 1995; Parkyn & Winterbourn 1997; Crowl et al. 2001; Heartsill-Scalley & Aide 2003). Parkyn & Winterbourn (1997) showed that exotic and native leaf-packs supported large numbers of invertebrates in a small headwater stream in the South Island of New Zealand. Moreover, in Chapter 2, I showed how coarse particulate organic matter (CPOM) was a potential driver of first- and second-order stream community structure. For example, EPT (mayflies, stoneflies, and caddisflies) richness and density, and shredder density decreased with decreasing benthic CPOM biomass, which declined rapidly within pasture downstream of forest. In addition, pastoral macroinverterbrate communities, associated with downstream decreases in CPOM, became increasingly different from forest communities with increasing distance downstream (see Chapter 2). However, the question remains: was terrestrial CPOM acting as a key driver of stream community change in these streams, or were other drivers (e.g., water temperature) more important? If CPOM is an important driver, the distance that leaf litter and woody debris are transported downstream of forest fragments may be an important determinant of the macroinvertebrate communities that reside in downstream pastoral reaches.

In this chapter, I examine the response of pastoral stream macroinvertebrate communities to additions of allochthonous resources (i.e., leaves and wood). This was to investigate whether allochthonous resources could facilitate a reset effect in community

structure. I predicted that a continuous input of leaf litter (simulating the allochthonous inputs of a forest) would increase habitat and food-resources, and promote the colonisation of more diverse, forest specialist, taxonomic groups (Fig. 4.1). Secondly, in order to investigate the distance forest-derived litter travels in streams, I measured transport distance of marked allochthonous resources downstream of forest. This was done to gauge the potential distance that streams export terrestrial organic matter downstream of their forest source relative to discharge and therefore the capacity of organic matter to drive community structure downstream of forests (see Chapter 2). Understanding allochthonous export patterns could help us predict how far apart patches of riparian vegetation need to be planted, in order to maintain continuous diverse macroinvertebrate communities.

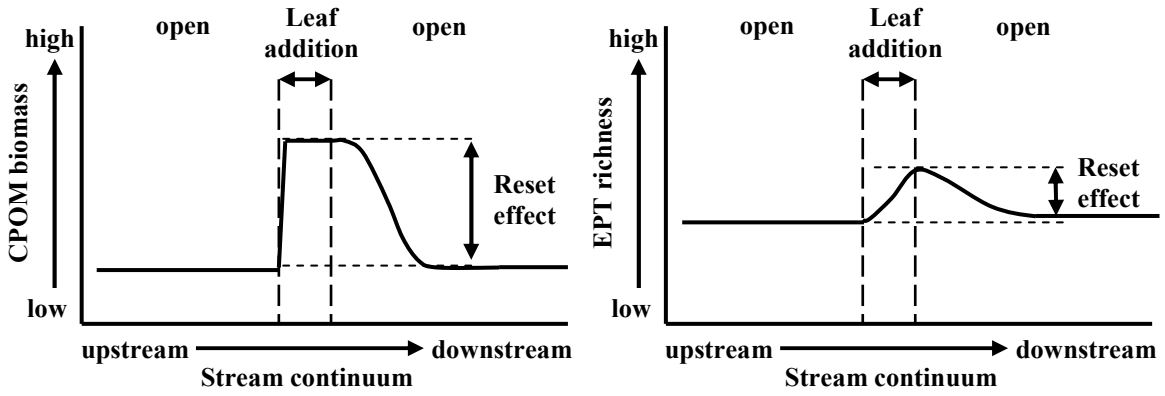


Figure 4.1 Hypothetical model of a potential "reset effect" brought about by leaf litter addition, and the downstream effect on CPOM biomass (left) and EPT richness (right), within a pastoral stream system.

4.2 Methods

4.2.1 Study sites

CPOM addition and transport experiments were conducted during base-flow conditions in four, first- and second-order streams in Canterbury. Two of the study streams, Lower Farm Stream and Binser Stream, were tributaries of the upper Waimakariri River and were located in the Cass Basin, 500–600 m a.s.l. (Fig. 4.2). These streams originated from continuous native forest dominated by mountain beech (*Nothofagus solandri* var. *cliffortioides*), with small isolated stands of red beech (*Nothofagus fusca*). Below the forest margin, each stream flowed through open grassland consisting of introduced pasture and native tussock (*Chionochloa* spp.) grazed by sheep (Wardle 2002). The other two study streams, Maungati

Stream and the upper Motukaika River, were located in the foothills of Stravon Station, near Mt. Nimrod, South Canterbury, at 300–400 m a.s.l. (Fig. 4.2). These two streams flowed from native broadleaf–podocarp forest fragments, dominated by totara (*Podocarpus* spp.) with scattered rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), and kahikatea

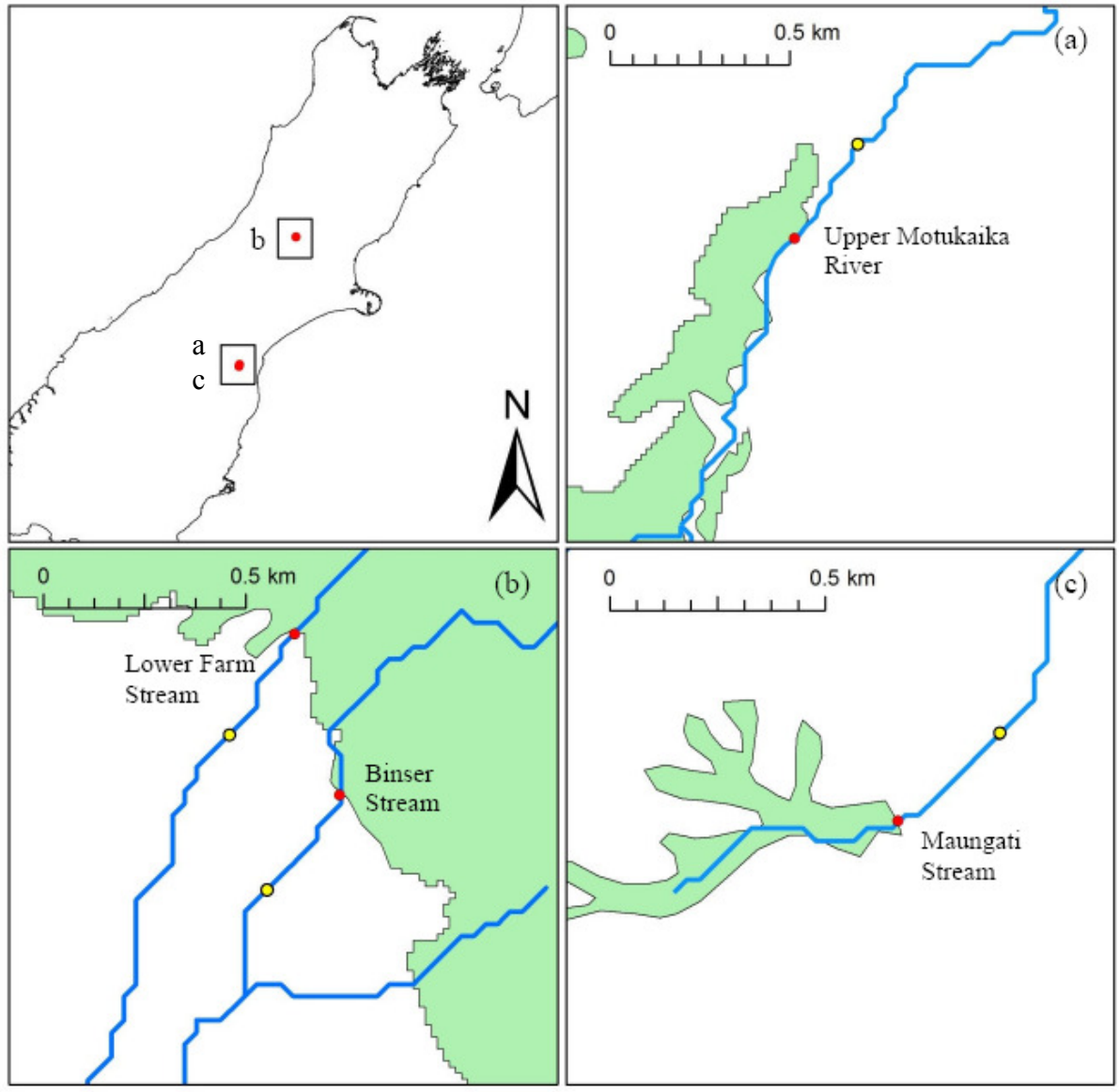


Figure 4.2 Four streams sampled throughout Canterbury (see inset) flowing from forest (green areas) into pasture (white areas). The two study areas were (a & c) Mt. Nimrod, South Canterbury; and (b) Cass Basin. The red symbols indicate where marked leaves and wood were added to streams at the forest edge for transport experiments, and yellow symbols indicate sites 300 m downstream from forest where leaf litter was added to streams for six weeks to test for macroinvertebrate community responses.

(*Dacrycarpus dacrydioides*). Both streams flowed into introduced pastures (e.g., ryegrass, white and red clovers) with moderate-intensity sheep and/or beef grazing (Norton & Fuller 1994; Wardle 2002).

4.2.2 Litter transport experiment

Leaf litter and woody debris transport experiments were carried out from the 11 January to 23 February 2010. In late December 2009, red beech leaves were collected from the Cass Basin. Red beech was used because its leaves have slow to moderate stream-breakdown rates (23 days to 50% weight loss; Parkyn & Winterbourn (1997)), and were expected to be large enough (approximately 4 cm length) to be located by the naked eye once dispersed in water (Fig. 4.3). Leaves were air dried for approximately four weeks. Once completely dried, 2,000 whole, undamaged leaves were selected, coated with fluorescent pink, acrylic spray-paint (Fig. 4.3) and allowed to dry. Marked leaves were then soaked in water for 24 h to make them neutrally buoyant.

Concurrently, 20 treated, pine dowels (2 m long, 12 mm diameter) were also marked with fluorescent pink, acrylic spray paint and allowed to dry. Each dowel was then cut into 20, 10 cm lengths (Fig. 4.3). The manufacturer's chemical treatment to waterproof the wooden dowels made them positively buoyant, and therefore, all dowels were boiled and soaked in water for at least 48 h prior to release.

On 11 January 2010, 500 marked leaves and 100 marked dowels were released into each stream channel at the forest edge. The number of leaves and dowels transported were counted within 50 m segments, up to 600 m downstream of the release point, at 48 and 96 h post-release, and then weekly for 4-6 weeks. The transport of wooden dowels was measured for up to 6 weeks; however, because mechanical abrasion accelerated the breakdown of leaves I had difficulty accurately tracking individual leaves late in the trial. Therefore, leaf transport measurements were recorded for only 4 weeks. The number of leaves and wood recorded in each 50 m reach were converted to the proportion of the total number of leaves and wood found along the entire 600 m study length of each stream.

4.2.3 Leaf litter addition experiment

In-stream leaf litter manipulations were carried out in the same study streams and at the same time as the litter transport experiments. In Chapter 2, I showed there was virtually no benthic CPOM 300 m downstream of the forest edge. Therefore, leaf litter additions were carried out 300 m below the forest (hereafter referred to as 0 m).

Figure 4.3 Above left: 10 cm wooden dowels, coated in fluorescent pink spray paint, used in wood transport trials; Above right: wooden dowels as they appear in the water column of the upper Motukaika River; Bottom left: marked red beech leaves used in leaf transport trials; Bottom right: marked leaves in Maungati Stream, 48 h after the addition.

One week prior to leaf litter additions, mountain beech leaves were collected from forests at Cass for the manipulation of Lower Farm and Binser streams, and a variety of native broadleaf species leaves were collected from forests at Mt. Nimrod, for the manipulation of Maungati Stream and the upper Motukaika River. These different leaf species were used to mimic the natural vegetation present in the catchment of each stream. This was to maintain any adaptations that macroinvertebrate species may have to leaf litter from their respective upstream catchment. Leaves were placed in large plastic bins and soaked in water for approximately one week prior to release to ensure neutral buoyancy and promote retention at the addition sites. Approximately 50 L of leaf litter was added to each stream, except Maungati Stream to which only 10 L was added because of its small size.

Prior to the release of leaf litter, the benthic macroinvertebrate community and CPOM (> 500 µm) biomass was surveyed. Three replicate Surber samples (0.096 m², 250 µm mesh) were taken in riffles and runs at a control site (i.e., 25 m upstream of the litter addition sites or -25 m), at the leaf litter addition site (0 m), and at three sites further downstream (100, 200 and 300 m). A single composite kick-net sample was also taken from a variety of habitats at each site to characterise macroinvertebrate diversity.

A further 50 L of leaf litter was added to each study stream each week for the following 6 weeks. One week after the final addition, another three replicate Surber samples and a composite kick-net sample were taken at the control site (-25 m), at the leaf litter addition site (0 m), and at the three sites downstream of the litter addition (100 m, 200 m and 300 m) to determine whether there had been any benthic community response and to quantify CPOM presence at each site.

4.2.4 In-stream physical variables

A number of in-stream physical variables were measured at the forest edge and at 6 sites downstream every 100 m. Water velocity was measured weekly with a flow meter (FLO-MATE™ 2000) at five points across the channel, four-tenths of water depth above the stream bed (Harding et al. 2009). Stream wetted width and depth were also measured at five points weekly at each site. Stream discharge was estimated per site using the formula:

$$\text{Discharge} = \text{cross-sectional water area } (m^2) \times \text{mean water velocity } (ms^{-1}).$$

Stream temperature was measured (YSI 550A DO meter) immediately prior to Surber sampling, both before and after CPOM additions. Sediment depth, substrate size, and the frequency of debris dams were measured within each 50 m segment downstream of forest, at the beginning of the experiment. Substrate size was measured by recording the length of the longest axis of 30 randomly selected cobbles. The thalweg length of each stream reach was measured with a handheld GPS unit (Garmin xTrexH) in the field, and the linear length of each 100 m reach was established using GIS techniques (ESRI ArcGIS 9.3). From these data, channel sinuosity between each stream site was estimated using the formula:

$$\text{Sinuosity} = \text{thalweg length/straight-linear length of reach.}$$

4.2.5 Macroinvertebrate and CPOM processing

In the laboratory, Surber samples were sub-sampled due to extremely high macroinvertebrate densities. However, the entirety of each Surber sample was also scanned and any additional taxa not found in the sub-samples were added to the species lists, along with data from the kick-net samples. Each of the Surber sub-samples was rinsed thoroughly through a 250 μm mesh sieve to remove excess sediments and its contents were transferred to a Bogorov tray for counting and identification, under a low-powered (10x magnification) dissecting microscope (KYOWA model sdz-pl). Macroinvertebrates were identified to species, where possible (Towns & Peters 1996; Smith 2003; Winterbourn et al. 2006). However, many early instars or damaged specimens lacked the necessary physical features to key them to species, and these individuals were instead classified to genus or family.

All CPOM from Surber samples was placed in foil weigh boats and dried at 50ºC for at least 48 h. Once dried, samples were ashed at 550ºC for 4 h and average ash-free dry weight (AFDW, ± 0.001g) of CPOM was calculated for each site.

4.2.6 Statistical analyses

Organic matter transport

Linear mixed-effects (LME) models (using the *lme4* package in R version 2.9.2.; R Development Core Team 2009), tested with maximum likelihood (ML), were used to explore the amount of variation in the proportion of wood and leaves explained by the fixed effects of distance from their release site (m) and time since their release (48, 96, 168, 336, 504, and 672 h), while accounting for variation due to differences among study streams (random effect). I used model simplification to estimate the *P* values and test the significance of the fixed effects, distance from release and time since release, and their interaction. That is, the main and interaction effects were removed from each LME model one-by-one, and using ML, the Chi-square (χ^2) statistic and its significance level was estimated (Crawley 2007).

The effects of stream discharge, average substrate size, channel sinuosity, and debris dam frequency on average CPOM transport length, was tested using separate linear regressions (small sample sizes prevented the use of multiple linear regression). Average CPOM transport length was calculated as:

Average transport length = sum (proportion wood or leaves x upper range distance),

where the proportion of total leaves or wood found in each 50 m reach was multiplied by the upper distance value of the reach they were found (e.g., at a distance interval of 50-99 m, the corresponding proportion would be multiplied by 99), and summed across all reaches in the stream.

Leaf litter addition

Prior to analyses, macroinvertebrates were grouped into taxonomic orders and functional feeding groups (shredders, scrapers, collector-browsers, predators, herb-piercers and filter-feeders) (Quinn et al. 2004; Mike Winterbourn pers. comm.). To test the effect of leaf addition on benthic CPOM biomass and benthic macroinvertebrate responses, a BACIP (Before-After Control-Impact Paired) design was used (Smith 2002). The BACIP approach compares a site before and after a treatment effect while accounting for natural change by pairing the impact area to another control area (Stewart-Oaten et al. 1986). CPOM biomass data were square-root transformed along with shredder density, whereas other macroinvertebrate response parameters, including total macroinvertebrate density, EPT density, and total macroinvertebrate richness, were log transformed. The BACIP design tested the categorical predictors of time, treatment type, and their interaction against each response variable and accounted for the random effect of variation between independent streams using LME models. Model simplification was used to test the main and interaction effects of time and treatment as for organic matter transport (above). Time was accounted for in the model as before leaf litter was added to streams and six weeks after. Treatment type was classed as control (-25 m; upstream of leaf addition) and treatment (0 m; at the site of leaf addition). The interaction effect between time and treatment indicated whether a significant effect of leaf addition on CPOM biomass and macroinvertebrate indices occurred over and above that caused by natural variation.

A simple linear regression model was used to determine whether the addition of leaf litter had an effect on stream benthic CPOM density downstream. This was performed using CPOM biomass data collected at the treatment site and 100, 200 and 300 m downstream. CPOM biomass was square-root transformed to meet assumptions of normality and homogeneity of variances, and tested against distance downstream from the leaf addition point.

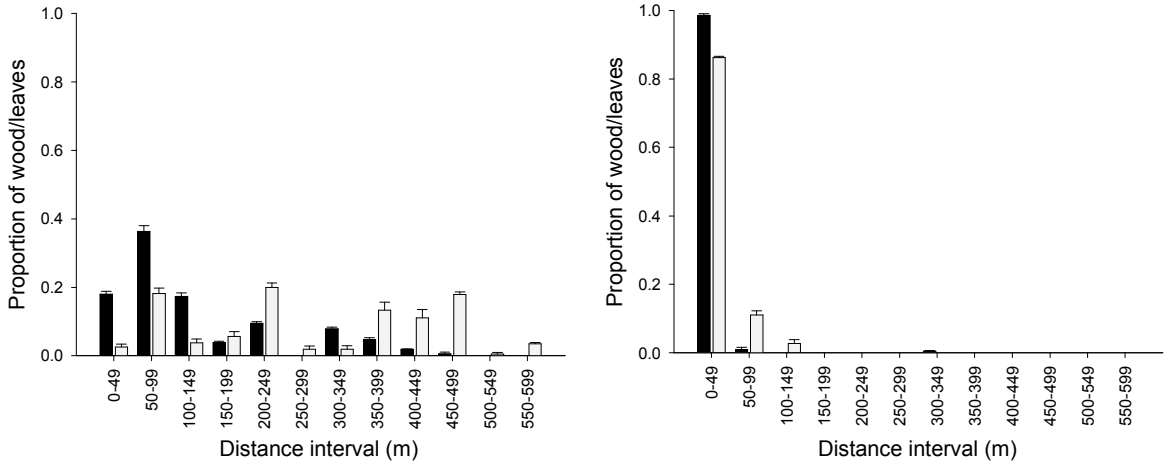
4.3 Results

4.3.1 How far was organic matter transported?

In three of the streams where marked leaves and wood were added, 80-100% of leaves and 90-100 % of wood were transported < 50 m downstream, over 4 and 6 weeks, respectively. However, CPOM was transported further in Lower Farm Stream with 48% of leaves moving 300–600 m downstream and 46% of wood being transported beyond 100 m over the entire study period. Differences in the proportion of both leaves and wood found at each distance did not change over the 4-6 weeks of surveying (Fig. 4.4, Table 4.1).

Lower Farm Stream had significantly higher discharge than the other three streams ($F_{3,24}$ = 20.04, P < 0.001). This coincided with a greater average transport distance of both wood and leaves, compared with the other study streams (Fig. 4.5). However, the overall effect of discharge on leaf and wood transport distance was not significant (wood $F_{1,16}$ = 2.34, P = 0.266; leaves $F_{1,16}$ = 2.35, P = 0.265) and may have been due to the low replication of sites. No significant relationship of average distance travelled by wood or leaves was detected with average substrate size (wood $F_{1,16}$ = 2.13, P = 0.282; leaves $F_{1,16}$ = 2.16, P = 0.280), channel sinuosity (wood $F_{1,16}$ = 0.08, P = 0.807; leaves $F_{1,16}$ = 0.09, P = 0.794), or the number of debris dams (wood $F_{1,16}$ = 0.71, P = 0.489; leaves $F_{1,16}$ = 0.67, P = 0.498).

(a) (b)



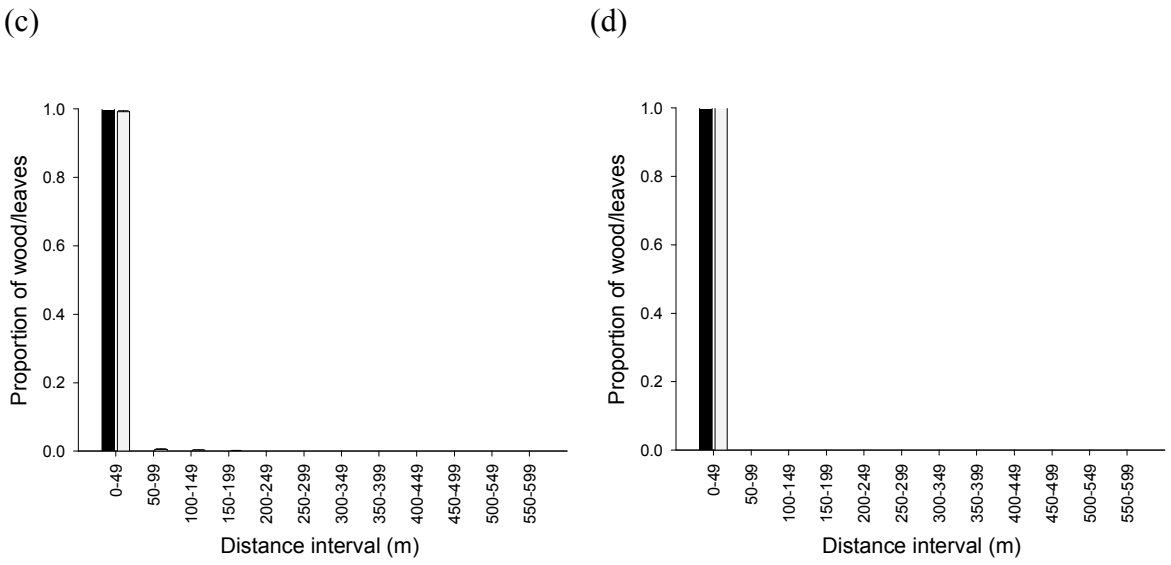


Figure 4.4 Mean (± 1 SE) proportional distribution of wood (black bars, $n = 8$) and leaves (grey bars, $n = 6$) measured weekly over 4 (leaves) or 6 (wood) weeks, within each 50 m reach downstream of the forest edge release site in (a) Lower Farm Stream, (b) Binser Stream, (c) Motukaika River, and (d) Maungati Stream.

Table 4.1 Results obtained with mixed effects models used to analyse variation in the proportion of wood and leaves transported over the time since their release and the distance from their release site. Significant *P* values (< 0.05) are indicated in bold.

Response	Effect variable	Variance	d.f.	χ^2	*P*
Proportion of wood transported	Stream (random)	0.04			
	Time		1	< 0.01	> 0.999
	Distance		1	82.26	**< 0.001**
	Time x Distance		1	< 0.01	> 0.999
Proportion of leaves transported	Stream (random)	0.04			
	Time		1	< 0.01	> 0.999
	Distance		1	47.04	**< 0.001**
	Time x Distance		1	< 0.01	> 0.999

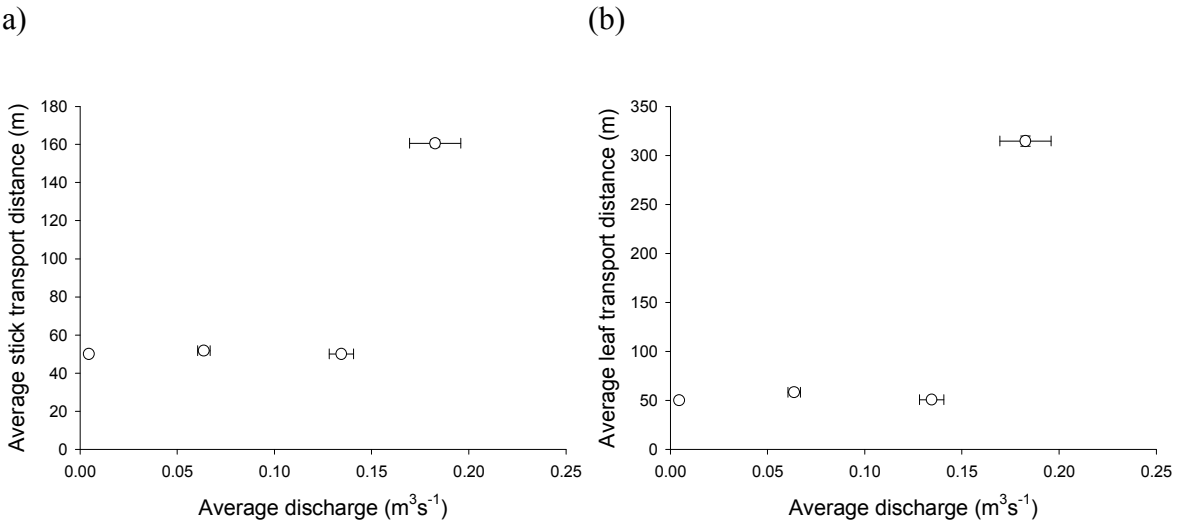


Figure 4.5 Mean (± 1 SE, wood *n* = 8, leaves *n* = 6) transport distance of (a) wood and (b) leaves in four streams with increasing mean (± 1 SE, wood *n* = 9, leaves *n* = 7) stream discharge over a 6-week period.

4.3.2 Leaf litter addition

Mixed effects models showed that CPOM biomass increased significantly as a result of the leaf addition, but remained relatively unchanged at the upstream control sites (Table 4.2). CPOM biomass at the addition sites increased markedly from about 4 g per m^2 AFDW to 156 g per m^2 ADFW after 6 weeks of leaf additions (Fig. 4.6a). This increase in CPOM was followed by a significant exponential decline in biomass over 300 m downstream, by which CPOM levels returned to control site levels ($F_{1,13}$ = 15.68, P = 0.002) (Fig. 4.6b).

A total of 55 macroinvertebrate taxa were collected from all streams before and after leaf additions (Appendix 3). Macroinvertebrate richness and EPT richness were similar at the control and treatment sites and did not change significantly over time (Fig. 4.7a & c, Table 4.2). Conversely, macroinvertebrate density, EPT density and shredder density all increased in response to the leaf-litter addition (Fig. 4.7b, d, e, Table 4.2). Over six weeks, total macroinvertebrate density increased by 196% at litter addition sites, whereas macroinvertebrate density at the control sites only increased by 84% (Fig. 4.7b). Meanwhile, EPT density increased by 137% at treatment sites compared to 89% at control sites (Fig. 4.7d). Likewise, shredder density also increased more at treatment sites (before: 3.5 per m², after: 6.9 per m²) than control sites (before: 0 ind. per m², after: 1.7 ind. per m²) (Fig. 4.7e).

However, none of these changes were statistically significant (Table 4.2), probably due to low site replication and a subsequent lack of statistical power.

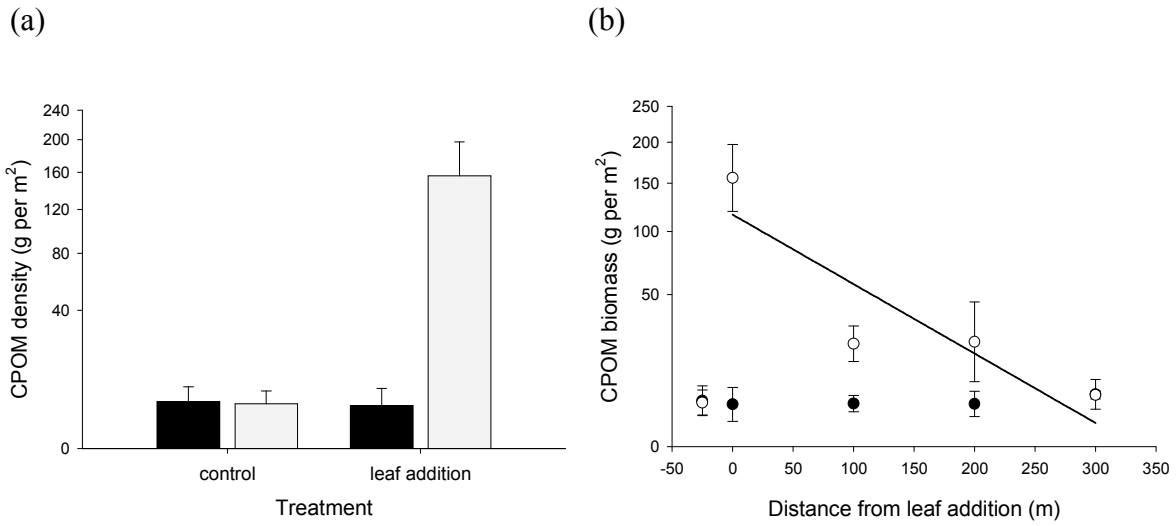


Figure 4.6 Mean (± 1 SE, $n = 4$) (a) CPOM biomass in streams at control and leaf-litter addition sites before (black bars) and six weeks after (grey bars) litter additions; and (b) CPOM biomass upstream of the litter addition site (-25 m), at the litter addition site (0 m), and 3 sites downstream of the litter addition site before (closed symbols) and six weeks after (open symbols) litter addition. The fitted line ($R^2 = 0.59$) is based on a linear regression testing how far CPOM (square-root transformed) was transported downstream (m) from the leaf-litter addition sites (0 m).

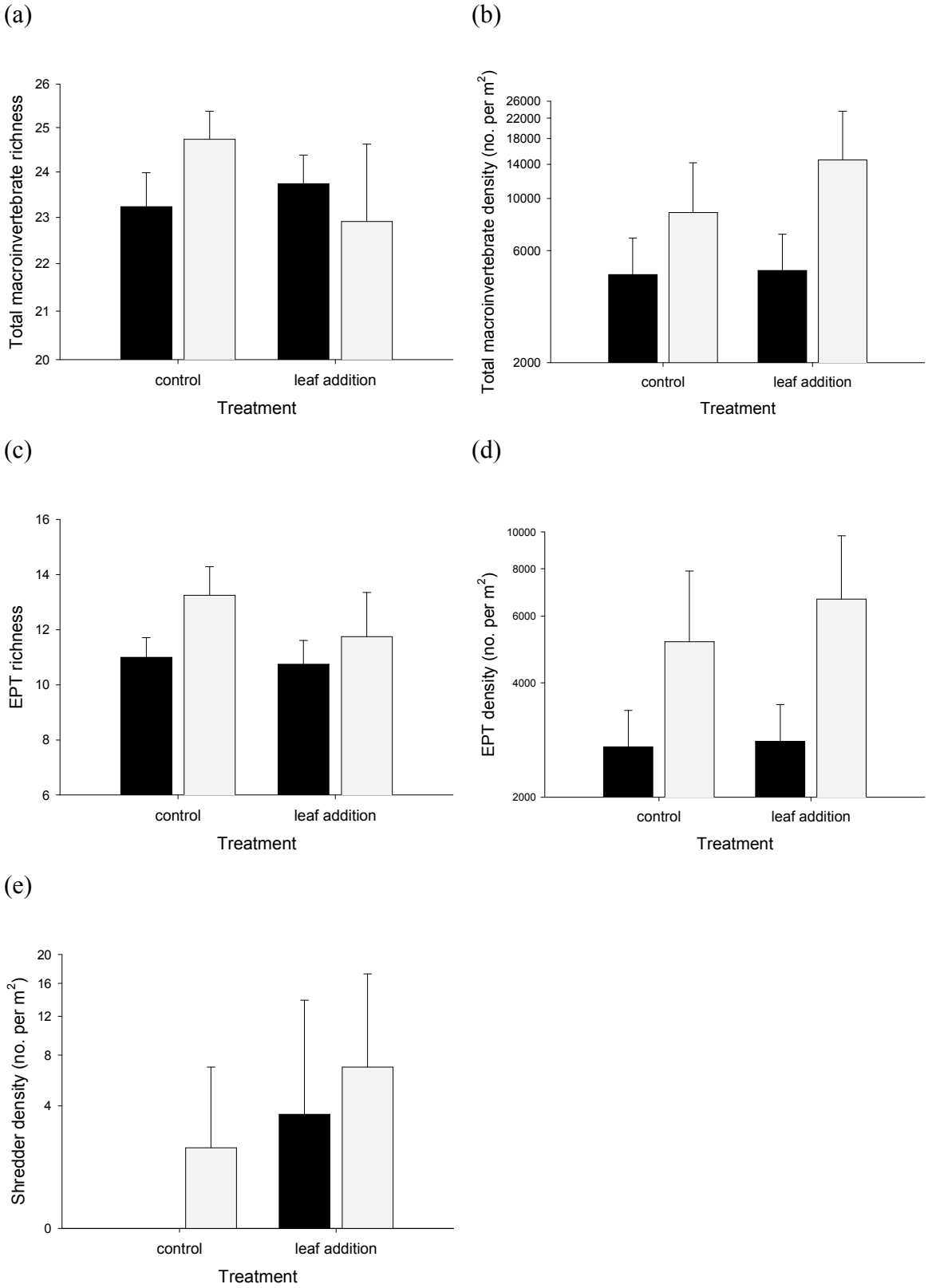


Figure 4.7 Mean (± 1 SE) (a) benthic macroinvertebrate richness, (b) macroinvertebrate density, (c) EPT density, (d) EPT richness, and (e) shredder density measured in four streams at control and leaf-litter addition sites before (black bars) and six weeks after (grey bars) litter additions.

Table 4.2 Statistical parameters of mixed effects models used to analyse the variation in CPOM biomass, total macroinvertebrate richness and density, EPT richness and density and shredder density before and after leaf litter additions, at control (-25 m) and treatment (0 m) sites. Significant *P* values (< 0.05) are shown in bold.

Response	Effect variable	Variance	d.f.	χ^2	*P*
CPOM biomass (g AFDW)	Stream (random)	< 0.01			
	Time		1	8.362	**0.004**
	Treatment		1	8.15	**0.004**
	Time x Treatment		1	19.72	**< 0.001**
Total macroinvertebrate richness	Stream (random)	< 0.01			
	Time		1	0.12	0.727
	Treatment		1	0.48	0.488
	Time x Treatment		1	1.96	0.162
Total macroinvertebrate density (individuals per m²)	Stream (random)	0.64			
	Time		1	16.48	**< 0.001**
	Treatment		1	3.33	0.068
	Time x Treatment		1	3.18	0.075
EPT richness	Stream (random)	3.35			
	Time		1	6.36	**0.012**
	Treatment		1	2.21	0.137
	Time x Treatment		1	1.31	0.253
EPT density (individuals per m²)	Stream (random)	0.34			
	Time		1	15.89	**< 0.001**
	Treatment		1	1.19	0.275
	Time x Treatment		1	0.77	0.381
Shredder density (individuals per m²)	Stream (random)	3.50			
	Time		1	1.36	0.244
	Treatment		1	2.94	0.087
	Time x Treatment		1	0.10	0.754

4.4 Discussion

Intensification of pastoral farming in formerly forested land has had a major impact on the degradation of streams and rivers. The replanting of riparian vegetation is a popular mitigation measure for restoring the adverse effects of pasture on streams. However, in order for riparian restoration efforts to be successful in maintaining and conserving freshwater species, patches of riparian vegetation need to maximise specific in-stream conditions to

which stream biota primarily respond, and provide such conditions widely throughout the length of the stream. One example is to ensure that patches of riparian vegetation maximise in-stream allochthonous resources and their transport.

4.4.1 How far was litter transported?

The CPOM added to the study streams was generally exported less than 50 m downstream of the addition sites. The one exception was Lower Farm Stream, which had a significantly higher discharge relative to the other streams. Contrary to my expectations, higher discharge had no significant effect on the greater distance that leaves and wood travelled at Lower Farm Stream. Nevertheless, patterns suggested there may have been a discharge threshold between 0.14 m^3s^{-1} and 0.18 m^3s^{-1}, which facilitated a large increase in leaf and wood movement. Secondly, I expected there to be a continuous movement of leaves and wood downstream over time, but under baseflow conditions, most movement occurred within the first 48 h of the experiment, and there was little further transport of allochthonous matter over the next 6 weeks.

The high retention of the study streams within the first 50 m below forest, supports earlier findings in Chapters 2 and 3, which showed that benthic CPOM rapidly decreased downstream of forest edges in open pasture. Steart et al. (2002) found similar results in experimental trials where leaf litter of a variety of tree species, rarely travelled beyond 100 m within 6 h of being added to headwater streams in Australia. It is likely that periodic flood events are responsible for much of the movement of stream benthic CPOM. Surges in discharge and changes in velocity associated with floods disturb stream beds (Biggs et al. 1999) and entrain litter under stream banks where leaf litter and woody debris are stored (Dewson et al. 2007). In a study on the annual energy budget of Bear Brook, a small undisturbed second-order stream in the northeast of the United States, Fisher & Likens (1973) showed that 66% of energy available to the stream (almost all of which was derived from forest litter) was exported to downstream ecosystems, 23% being CPOM. Fisher & Likens (1973) suggested that this downstream export of organic matter was also governed by stream discharge.

In general, high organic matter retention is probably a consequence of the morphological profiles of small streams, their low discharge, and the physical nature of the vegetation entering them. In particular, several studies have shown that stream-specific morphology influences stream transport and retention (Bretschtko 1990; Mathooko 1995; Afonso & Henry 2002; Kraft & Warren 2003; Larranaga et al. 2003). Smock et al. (1989)

showed that organic debris dams stored between 21 and 85% of CPOM in two first-order streams in south-eastern Virginia. In experimental manipulations, they also found that increasing the abundance of debris dams in the streams increased organic matter storage, and resulted in an increase in both macroinvertebrate abundance, and the relative abundance of shredders (a reflection of the stored organic matter food-resource and the greater habitat stability of dams compared to shifting substrates). The structure of stream riffles, pools, and sinuosity can also affect CPOM transport. Nakajima et al. (2006) found that CPOM accumulation was controlled by the arrangement of stones projecting above the water surface in riffles, and by pools which experience low velocities at periods of high stream flow. They also found that higher average velocities on the outside of meandering bends create cross-stream currents that carry leaves to accumulate on the inner sides of bends where velocity is low. Although I measured discharge, substrate size, channel sinuosity and the number of debris dams in each study reach, I was not able to detect any effects of these factors on organic matter export. However, it is likely that the resolution of my measurements was not sufficient to estimate retention and transport accurately. Substrate size, for example, took no account of stream bed roughness or bed architecture. Some studies have suggested that stream bed morphology needs to be profiled extensively over entire reach lengths and widths (e.g., Nakajima et al. 2006).

Differences in the physical characteristics of leaves and wood of different forest tree species may also lead to differences in retention and mobility. A study on flotation differences between *Eucalyptus* and *Nothofagus* forest leaf species showed that differences in buoyancy were reflected in transport distances along a first order stream (Steart et al. 2002). As mentioned earlier, Steart et al. (2002) found that regardless of taxonomic group, no leaves travelled beyond 100 m in 6 h, however, some rainforest species were transported longer distances than others. Other studies have also attempted to quantify the distance that individual leaves are translocated downstream. Young et al. (1978) found that distances travelled by maple (*Acer rubrum*), beech (*Fagus grandifolia*) and oak (*Quercus rubra*) leaves ranged markedly from approximately 100 m to over 1 km in a woodland stream in Pennsylvania over approximately 3 weeks. Moreover, Jones & Smock (1991) showed that the mean transport of leaves in a first-order stream could be as short as 1.6 m after 2 h.

Care must be taken when extrapolating “rules of thumb” for stream transport based solely on stream physical characteristics. Simple measures of stream discharge, sinuosity, substrate size and dam frequency, as measured in this study, do not sufficiently quantify terrestrial litter transport. It is therefore necessary for researchers attempting to model organic

matter transport and retention rates in streams to take into account a variety of measures, such as stream-bed roughness, lateral and longitudinal flow profiles, leaf litter species and bank profiles.

4.4.2 Does the addition of leaf litter reset stream communities?

Streams in this study successfully retained added leaf litter resulting in marked increases of available benthic CPOM at addition sites. My results also showed that litter additions created a downstream subsidy effect, increasing CPOM biomass for 200 m downstream from addition sites. Increases in benthic CPOM biomass at leaf addition sites showed promising signs of an induced "forest reset effect" by increasing EPT and shredder densities. Although this result was not significant, it may have been due to the much longer response time macroinvertebrates require to respond to a change in allochthonous resources. Specifically, in-stream basal-food and habitat increases, created by the increases in CPOM, may need longer than 6 weeks to impact macroinvertebrate life-history processes. Following the additional subsidy of CPOM to reaches downstream of the litter addition site (i.e., at 100, 200 and 300 m), we might also expect macroinvertebrate densities to increase downstream.

Several studies have shown that macroinvertebrate communities shift as agricultural streams enter native forest (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006; Niyogi et al. 2007; Chakona et al. 2009). Scarsbrook & Halliday (1999) found changes in several macroinvertebrate biotic indices within 300 m of three first-order pastoral streams flowing through regenerating native forest. They also found that mean CPOM levels were higher at forested sites than pasture sites. However, their data suggested that water quality variables (e.g., conductivity and pH) were more important than CPOM in controlling changes in invertebrate community composition (Scarsbrook & Halliday 1999). In contrast, Wallace et al. (1997) observed several major changes in the abundance, biomass, and production of invertebrate fauna within a mixed substrate stream that had been experimentally-deprived leaf litter inputs for 3 years. They found that 17 of the 29 most abundant taxa, which provided 93-97% of benthic production, exhibited significant reductions in abundance and/or biomass during the leaf exclusion period. This resulted in a bottom-up trophic cascade that reduced the abundance of predators due to food limitation. Other studies both in New Zealand (Storey & Cowley 1997; Harding et al. 2006; Niyogi et al. 2007) and abroad (Chakona et al. 2009) have documented similar results to Scarsbrook & Halliday (1999), whereby water quality and macroinvertebrate structure has improved with increased riparian canopy downstream. These studies highlight the resilient nature of stream

communities and their ability to be restored and rehabilitated by riparian vegetation, but do not provide insights into what riparian mechanisms maintain forest communities. Understanding these mechanisms needs to be a management focus to better mitigate the adverse impacts of agriculture on New Zealand's freshwater ecosystems.

In addition to CPOM, other mechanisms have been suggested as potential drivers of stream ecosystem change in land-use studies. They include changes in sediment and nutrients (Quinn & Stroud 2002; Niyogi et al. 2007; Song et al. 2009), substrate composition (Wallace et al. 1997), light and temperature regimes (Davies-Colley 1997; Rutherford et al. 1997; Harding et al. 1999; Young et al. 2005), hydrology (Smith 1993), channel morphology (Sweeney 1993), habitat heterogeneity (Allan & Flecker 1993; Harding et al. 1998; Townsend et al. 2003) and algal production (Quinn et al. 1997; Bojsen & Jacobsen 2003). Evaluation of the potential functional mechanisms of riparian forest needs to be investigated in more stream systems and over longer time frames to enable invertebrate life-history processes to take effect. For example, Richardson & Neill (1991) suggested several generations of consumers are required to detect responses to detrital manipulations. More specifically, studies investigating the impact of CPOM on stream function and diversity should address its relative importance as a food resource as opposed to a habitat. Investigating the relative importance of specific species of wood and leaves on invertebrate structure such as breakdown rates and palatability is also important. Parkyn &Winterbourn (1997) found that the colonisation of leaves by shredders in a small headwater stream in the South Island was higher for willow (*Salix fragilis*) and red beech (*Nothofagus fusca*) than other leaf species, including elm (*Ulmus procera*) and mahoe (*Melicytis ramiflorus*). In laboratory trials, they also found that the facultative shredder, *Olinga jeanae*, showed a preference for elm and red beech leaves, which were the fastest to break down and had high respiration rates.

The above aspects emphasise the need for freshwater ecologists to further delve into the mechanistic relationships riparian buffers share with stream ecosystems. It is clear that leaf litter additions can bring about organic resource reset effects by increasing benthic CPOM in pastoral streams. However, the corresponding effect CPOM increases have on macroinvertebrate communities, and thus the function of terrestrial organic matter as a riparian mechanism restoring stream health, remains uncertain.

4.4.3 The role of CPOM in the management of pastoral streams

Thus far my discussion has highlighted the many aspects of stream morphology and species-specific leaf and wood characteristics that are important for litter transport and retention rates. Although testing the relationships of organic matter transport with many of these factors was not possible with my data, trends shown by the data and in other studies (e.g., Smock et al. 1989; Steart et al. 2002; Nakajima et al. 2006; Dewson et al. 2007) have led me to believe that discharge, in conjunction with many aspects of stream (e.g., longitudinal and lateral discharge and substrate profiles) and forest tree morphology (e.g., leaf buoyancy) play an important role in CPOM transport. Whether or not CPOM can facilitate forest ecosystem function and maintain in-stream diversity, it undoubtedly contributes to community structure. If an aim of riparian management is to maximise natural conditions in pastoral streams, the planting of riparian buffers should include native plant species, which produce litter and can maximise CPOM supply downstream. This will help maintain allochthonous food resources and diverse habitats in agricultural landscapes where it is not always feasible to plant riparian buffers. In this sense, it is possible that forest stream communities may be sustained temporarily for extended distances away from vegetated margins. To achieve this in New Zealand, research must move towards characterising species-specific, native forest leaf and wood transport rates by investigating the influence of such traits as leaf size, shape, and buoyancy on facilitating movement. At the same time, these attributes must be matched to longitudinal and lateral profiles of stream discharge, riffles, pools, and sinuosity. Scarsbrook & Halliday (1999) cautioned a management strategy using the discontinuous replanting of riparian forest cover, largely due to the warnings of Davies-Colley (1997) and Trimble (1997) who stated that riparian canopy restoration in streams may carry an increased risk of bank erosion as sediment deposits, previously stabilised by encroaching pasture grasses and aquatic macrophytes, become destabilised affecting downstream water quality and biota. Therefore, care must be employed for such management techniques and the long-term benefits of discontinuous planting weighed against the short-term negative effects.

Resource managers are currently limited by the lack of scientific knowledge on the mechanistic relationships shared between riparian systems and lotic ecosystems. If the preservation and conservation of threatened freshwater species is to be assured for the future, freshwater ecologists need to quantify the necessary structural characteristics that forest fragments and riparian buffers require in order to preserve their existence.

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Chapter 5: General discussion

Over the last 150 years New Zealand has experienced enormous shifts in land use. A country that was once primarily forested now has substantial areas dominated by intensive agriculture (McGlone 1989; Collier 1992). Forested landscapes, compared to agricultural landscapes, have been shown to markedly differ in stream sediment and nutrient concentrations (Quinn & Stroud 2002; Niyogi et al. 2007; Song et al. 2009), light and temperature (Davies-Colley 1997; Rutherford et al. 1997; Harding et al. 1999; Young et al. 2005), hydrology (Smith 1993), channel morphology (Sweeney 1993), habitat heterogeneity (Allan & Flecker 1993; Harding et al. 1998; Townsend et al. 2003), basal energy resources (Quinn et al. 1997; Townsend et al. 1997; Benstead et al. 2003; Bojsen & Jacobsen 2003), and aquatic communities (Scott et al. 1994; Harding & Winterbourn 1995; Boulton et al. 1997; Quinn et al. 1997; Ometo et al. 2000; Hall et al. 2001; Harding et al. 2006). Not surprisingly, much research has focused on comparisons between forested and agricultural catchments (e.g. Scott et al. 1994; Quinn et al. 1997), yet few studies have examined differences between upstream and downstream conditions in streams flowing between pasture and forest (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Harding et al. 2006; Niyogi et al. 2007). My study looked at how morphological, chemical and biological conditions changed over a forest-pasture gradient in small, headwater streams. In particular, I was interested in the ramifications of these changes for improving the effectiveness of riparian management.

5.1 The importance of forests for the maintenance of downstream freshwater communities

The interdependent processes occurring between a stream and its riparian forest can be decoupled due to anthropogenic changes to the terrestrial landscape (Collier et al. 1995; Quinn et al. 1997; Harding 2003). In New Zealand, much forested land has been converted to agriculture, primarily in lowland areas (Collier 1992). Consequently, many streams have forested headwaters but flow through pastoral landscapes in the lower reaches. Sudden losses of riparian forest can create downstream gradients in stream physico-chemical and biotic conditions. These changes include reductions in habitat heterogeneity, decreases in forest carbon inputs and allochthonous food sources (e.g., leaf litter and terrestrial arthropods), and increases in water temperature (Fig. 5.1). My research highlighted the importance of

continuous forest in upstream reaches and how this can assist in the maintenance of freshwater macroinvertebrate communities in modified landscapes downstream. Specifically, I found that a sharp transition in land-use change, from upstream forested catchments to downstream pasture, caused a gradient of increasing water temperature and a marked reduction in benthic coarse particulate organic matter (CPOM). Surprisingly, few other chemical and morphological changes were found despite assessing a total of 16 streams in two regions of New Zealand. As a result of these changes in downstream temperature and CPOM, total macroinvertebrate richness, EPT richness and macroinvertebrate densities decreased, and there was a general shift from evenly distributed allochthonous-based communities to autochthonous-based communities that were highly dominated by molluscs (Chapter 2).

Many studies have recognised that the distance CPOM moves downstream can typically be very short in small streams (e.g., Jones & Smock 1991; Steart et al. 2002). I found that headwater streams can be highly retentive and that CPOM transport was generally less than 50 m (Chapter 4). It is possible that this rapid decrease of stored CPOM below a forest edge can have a marked impact on macroinvertebrate community structure (i.e., change in composition from allochthonous- to autochthonous-based communities), and probably has important consequences for wider ecosystem function, such as stream food web structure (Wallace et al. 1997; Nakano et al. 1999; Nakano & Murakami 2001) (Fig. 5.1). In contrast to the rapid decreases seen in CPOM biomass below a forest's edge in my study, Fisher & Likens (1973) found that most of the energy (66%) available to a small headwater stream in the U.S. was exported downstream, most of which was derived from adjacent forest. This contrast is probably due to the fact that my study streams were particularly retentive because of prolonged low discharges. After reviewing the literature, I concluded that laterally and longitudinally profiling stream morphological features, such as substrate roughness and discharge, as well as quantifying the species-specific transport potential of leaves would provide an improved understanding of how small stream reaches retain terrestrial organic subsidies.

5.2 The importance of forest structure for in-stream communities in downstream pastoral reaches

Although the effect of forest fragmentation has been poorly examined in freshwater environments (Harding et al. 2006), the influence of forest structure and location potentially

have important consequences for stream ecosystems within and downstream of forest (Fig. 5.1). In particular, forest buffer width and length (Storey & Cowley 1997; Scarsbrook & Halliday 1999; Nakamura & Yamada 2005), vegetation type and height, and canopy density (Young et al. 1978; Davies-Colley 1997; Rutherford et al. 1997; Steart et al. 2002), as well as the physical nature of the in-stream channel (Smock et al. 1989; Davies-Colley 1997; Rutherford et al. 1997; Nakajima et al. 2006), have been shown to affect in-stream conditions (e.g., temperature regimes and allochthonous resource inputs) and subsequently, aquatic macroinvertebrates and food-webs within forest (Wallace et al. 1997; Nakano et al. 1999) (see top of Fig 5.1). However, the impact that upstream forest size and structure can have on downstream ecosystems in differing land-uses, such as pasture, has been largely neglected (see bottom of Fig. 5.1). In Chapter 3, I found that the rate of downstream change in macroinvertebrate community composition may depend on the size of the forest fragment upstream. Although both water temperature and CPOM availability changed significantly downstream of the forest fragments, temperature was the most important driver of change in community composition. Moreover, stream temperature increased more rapidly downstream of small- and medium-sized fragments than larger fragments, which coincided with a faster decrease in EPT taxa and a rapid increase in scraper densities in pastoral reaches. Macroinvertebrate communities within the pastures draining from small forest fragments were also dominated by mollusc scrapers, but communities within medium and large forest fragments had more even communities.

Davies-Colley (1997) and Rutherford et al. (1997) have shown that water temperature is strongly affected by riparian condition, and more specifically, the height and canopy structure of streamside vegetation. A number of studies have also recommended minimum riparian widths necessary to maintain the shading of streams. Nakamura & Yamada (2005) have suggested a riparian buffer width of 15-20 m be preserved to maintain shading in Japanese streams. Others have suggested a buffer width of 30 m in the western U.S. (Brazier & Brown 1973; Spence et al. 1996) and 10-20 m in the eastern U.S. (Aubertin & Patric 1974). However, there remains little consensus on how wide riparian buffers should be. Some New Zealand forest is typically very shady and gradients of light exposure have been found to be abrupt, with high light levels in pasture diminishing to low light conditions in as little as 10 m into the forest (Davies-Colley et al. 2000). In conjunction with buffer width, forest length is also important for the health of forest stream ecosystems. Scarsbrook & Halliday (1999), for example, found that water quality variables, CPOM, and aquatic invertebrate communities recovered from pastoral effects approximately 300 m into native forest. As a

proximate measure for forest length and width, my study indicated that forest size may also impact stream condition and macroinvertebrates living downstream of forest margins in open pastoral landscapes. Specifically, a forest patch as small as 7 ha in size can maintain stream benthic CPOM levels similar to a large forest patch (e.g., 20–100 ha in size), yet a large forest patch (> 100 ha) may be required to maintain cool water temperatures for a long distance below a forest in pasture. Additionally, I found that a mid- or large-sized forest fragment (e.g., > 20 ha) can maintain community evenness and may restrict pastoral taxa dominance in macroinvertebrate communities within and downstream of it (Chapter 3). However, the impact of a forest's size on a stream ecosystem is relative to the physical nature of the stream flowing through it (Fig. 5.1). For example, a larger stream requires a taller and/or larger canopy to shade a greater area exposed to solar radiation (Davies-Colley 1997; Rutherford et al. 1997).

5.3 The importance of terrestrial carbon inputs for the maintenance of stream biodiversity

Streams are open ecosystems and energy can enter a stream either as solar radiation (promoting autochthonous or algal resources) or as organic matter (providing allochthonous resources) (Fisher & Likens 1973). In particular, small first- and second-order headwater streams in forested landscapes are strongly heterotrophic, and several North American studies have shown that detrital inputs from surrounding forest far outweigh in-stream primary production (Fisher & Likens 1973; Webster et al. 1995; Wallace et al. 1997). For example, Fisher & Likens (1973) suggested that 99% of the annual energy input to a small forested North American stream was allochthonous, 44% of which was accounted for by litter and throughfall from the adjacent forest. In Chapter 4, I found that adding leaf litter could essentially reset the amount of stored benthic CPOM in a pastoral stream to that of a forested reach. Although unclear, there was a weak trend of increased macroinvertebrate numbers, including EPT and shredders, associated with litter additions, suggesting that leaf litter additions may have a significant, positive effect on in-stream macroinvertebrate community structure.

Allochthonous inputs have an important function in the maintenance of forest stream food-webs (Fig. 5.1). Wallace et al. (1997) showed that terrestrial litter inputs were closely linked to multiple stream trophic levels, having a strong bottom-up control on the abundance

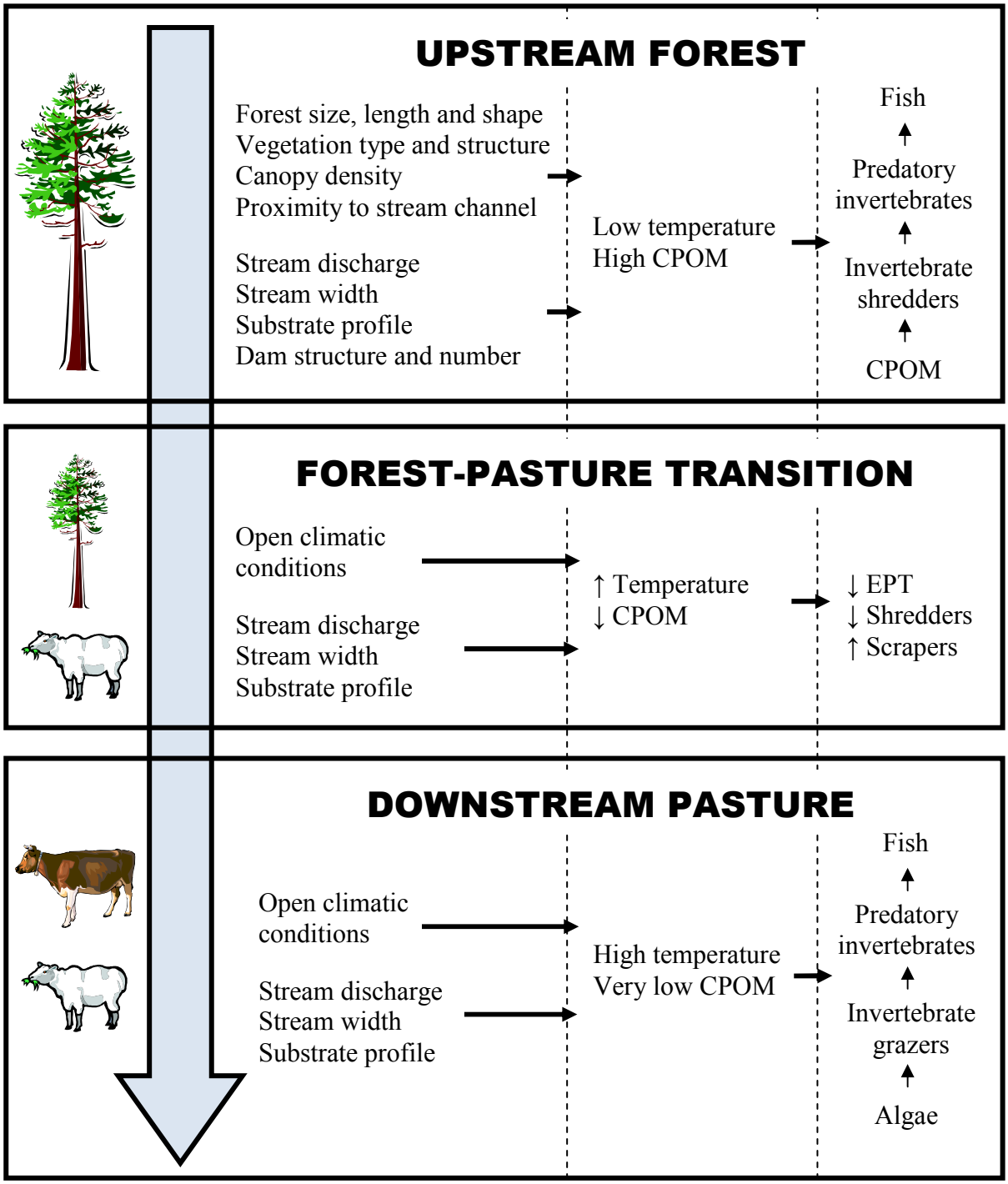

Figure 5.1 Overview of the longitudinal changes in the drivers (e.g., water temperature and CPOM) of community structure and composition within the forest, at the forest-pasture transition zone, and within the pastoral landscape downstream of forest fragments.

of higher order consumers. Furthermore, by excluding litter inputs into a stream, Wallace et al. (1997) reduced the abundance and biomass of large- and fine-particle-feeding detritivores and showed that this reduced the number of predators. Nakano et al. (1999) also

demonstrated strong trophic interactions across forest-stream ecosystem boundaries in a large-scale exclusion of terrestrial arthropods and predatory fishes from a Japanese stream. They showed that when forest arthropod inputs into the stream were experimentally reduced, fish predation pressure shifted from terrestrial to aquatic prey and resulted in a subsequent trophic cascade. Fish predation reduced the number of aquatic arthropods, which in turn led to an increase in periphyton biomass due to decreased grazing pressure by the arthropods.

The contribution of large woody debris to streams can also increase stream habitat heterogeneity by providing structure, altering flow patterns, enhancing sediment deposition, forming pools and retaining organic matter (Bis et al. 2000; Cordova et al. 2007; Schneider & Winemiller 2008). Lester et al. (2007) suggested that the wood addition to 8 pastoral streams in Victoria, Australia, created greater habitat complexity within the stream ecosystem. In turn, the increased habitat complexity supported higher overall macroinvertebrate richness, more pollution sensitive taxa, and a greater diversity of functional feeding groups.

5.4 Implications for riparian management mitigating pastoral impacts on freshwater ecosystems

Historically, agriculture has been one of the most important sectors of New Zealand's economy, and the demand for agricultural land has had a major influence on the country's streams and rivers. More recently, there has been a shift towards developing a broader view of the value of streams and rivers, with an increased appreciation of the need to restore and rehabilitate freshwater ecosystems (Collier et al. 1995). But the limitations on remediating pastoral catchments are numerous and challenging. For example, the replanting of riparian vegetation is a widely accepted restoration approach, however, the scientific, financial, and societal foundation for such an approach is not as strong as it should be. Therefore, there is a growing demand for the development of innovative approaches in riparian management to mitigate agricultural impacts efficiently.

Replanting entire pastoral catchments is rarely possible, and Scarsbrook & Halliday (1999) instead proposed the use of discontinuous riparian patches for mitigating the adverse agricultural impacts on streams. However, my results show that in order to maintain continuous stream health along a stream, small riparian patches would most likely have to be planted in close proximity to one another. In Chapters 2 & 3, I found that stream conditions changed rapidly downstream from forests, and usually within a few hundred metres (Chapter 2 & 3). I found stream temperatures increased rapidly, while CPOM biomass decreased

causing a shift in benthic macroinvertebrate communities, and a loss of forest-dwelling taxa. These results highlight important implications for establishing a balance between the lengths of forested versus non-forested reaches along a managed stream. If degradation occurs more rapidly in forest to pasture transitions (i.e., temperature increases, CPOM decreases) than recovery does in pasture to forest transitions, then there would be a proportional net loss in stream health with increasing distance downstream. Scarsbrook & Halliday (1999) found that CPOM and invertebrate communities recovered from pastoral effects approximately 300 m into native forest. In conjunction with my results, this suggests that first-order streams are highly resilient and that perhaps the recovery of streams upon re-entering forest occurs just as quickly as degradation upon entering pasture. Nevertheless, the speed of recovery will be influenced by a number of factors, such as the size and shape (or length) of the forest fragment, proximity of the fragment to the stream channel, isolation of refuge forest fragments to one another, and the vegetation and canopy structure of a riparian zone. My study showed a forest size effect on the rate of macroinvertebrate community dominance by molluscs downstream (Chapter 3). This suggests that replanting larger forest areas may possibly maintain the stream health of pasture reaches further downstream than that of smaller forest areas. Consequently, this means that larger riparian patches could potentially be planted further apart (Fig. 5.2).

The mechanisms of community change under riparian conditions have also been poorly studied. Numerous measures of stream condition have been shown to drive in-stream community structure but few studies have isolated and tested the direct effects of these mechanisms on community responses. An underlying theme throughout my research was the role of terrestrial CPOM and temperature as major drivers structuring forest benthic macroinvertebrate communities. The manipulation of litter biomass in pastoral reaches showed promising improvements in community responses (Chapter 4). This suggested that targeting riparian management schemes that maximise forest terrestrial carbon inputs into streams may improve the ability of habitat reaches in and downstream of riparian zones to act as refuges for forest species. The type of riparian vegetation planted needs to provide invertebrates with both short- and long-term food resources and in-stream habitat. This could be achieved by planting a mixture of deciduous and evergreen trees with high litter turnover rates. In terms of the discontinuous replanting of riparian vegetation, maximising the transport of this litter downstream, through selecting plant species with morphological features suited for high export, could mean macroinvertebrate communities are maintained further downstream of forested reaches and therefore forest could be planted further apart.

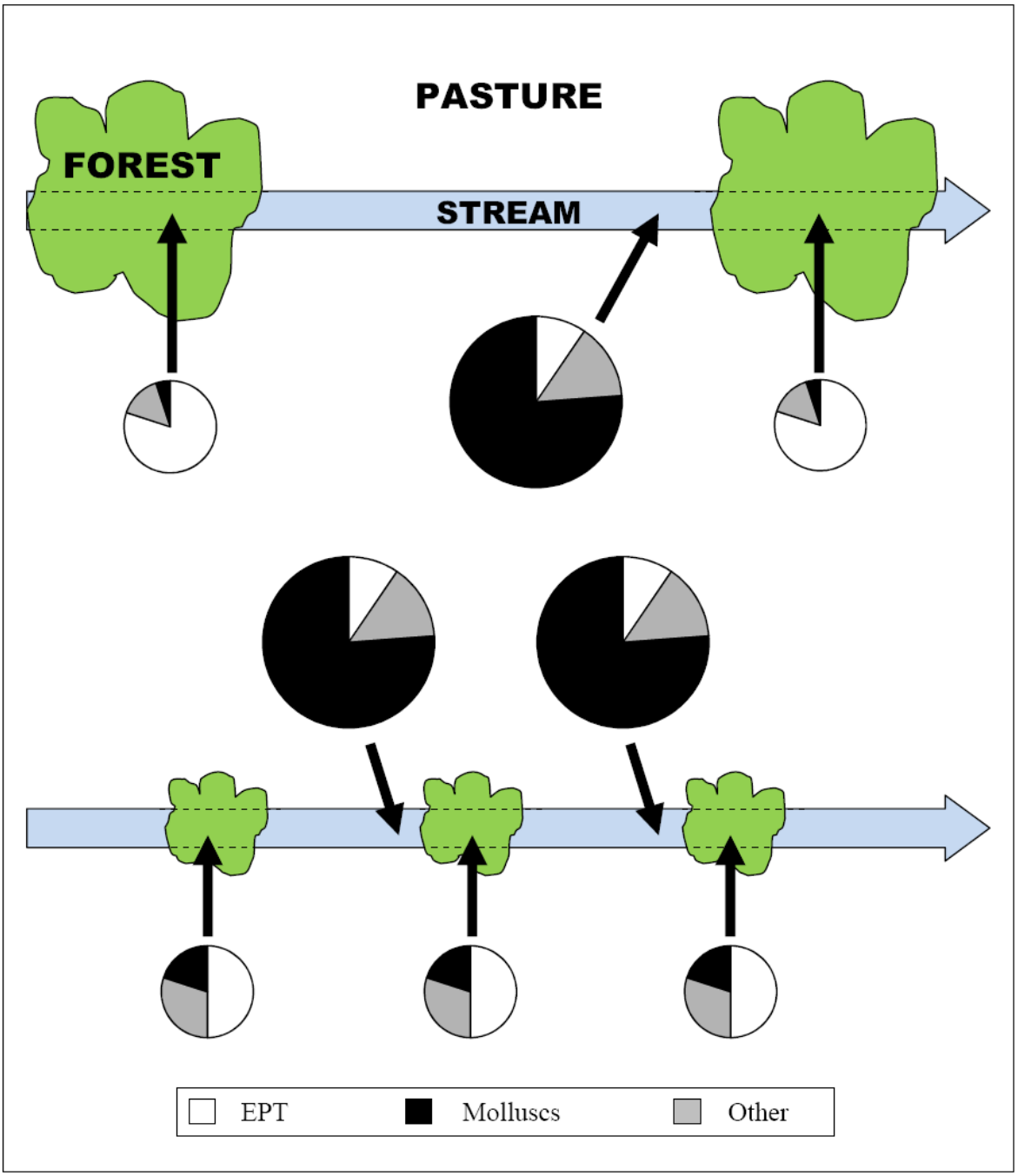

Figure 5.2 Hypothetical representation of possible community structures within and between discontinuous riparian forest patches. Larger pie charts represent larger in-stream macroinvertebrate densities. Larger fragments can be planted at further distances apart than smaller fragments because larger fragments can potentially restore pastoral stream communities greater distances downstream.

5.5 Conclusions

New Zealand's streams and rivers have important ecological, aesthetic, cultural, and recreational values and maintaining the health and diversity of these systems is a national imperative. However, the maintenance and preservation of the nation's freshwater ecosystems requires new and innovative approaches to mitigate the adverse effects that land-use change has had on natural waterways. Planting riparian vegetation in agricultural land has a valuable part to play in the maintenance and restoration of freshwater quality and the biota that live within streams and rivers. Yet the background knowledge behind the mechanistic relationships between streams and riparian vegetation remains limited and hinders any ability to effectively manage catchments. A greater understanding of these processes will likely enable resource managers and land owners to effectively and efficiently manage degraded ecosystems based on sound scientific knowledge.

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Appendices

Appendix 1 The presence (X symbol) or absence (no symbol) of aquatic macroinvertebrate orders, functional feeding groups and taxa collected from five streams at Mount Taranaki (see Chapter 2).

Order	Functional Feeding Group	Taxa	Digby Stream	Bull Creek	Fork Stream	Snag Stream	Cold Stream
Ephemeroptera	Predator	*Ameletopsis perscitus*		X			
	Filter-feeder	*Coloburiscus humeralis*	X	X	X	X	X
	Collector-browser	*Deleatidium* spp.	X	X	X	X	X
	Predator	*Ichthybotus hudsoni*		X		X	
	Collector-browser	*Neozephlebia scita*	X	X	X	X	X
	Collector-browser	*Nesameletus ornatus*	X	X	X	X	X
	Collector-browser	*Zephlebia* spp.	X	X	X	X	X
Plecoptera	Shredder	*Acroperla trivacuata*		X		X	
	Shredder	*Austroperla cyrene*	X	X	X	X	X
	Collector-browser	*Megaleptoperla diminuta*	X	X	X	X	X
	Predator	*Megaleptoperla grandis*					X
	Collector-browser	*Spaniocerca zelandica*	X	X	X	X	
	Predator	*Stenoperla prasina*	X	X	X	X	X
	Collector-browser	*Taraperla pseudocyrene*	X	X	X	X	X
	Collector-browser	*Zelandobius* sp. 1	X	X	X	X	X
	Collector-browser	*Zelandobius illiesi*	X		X		
	Collector-browser	*Zelandoperla decorata*	X	X	X	X	X
Trichoptera	Filter-feeder	*Aoteapsyche* spp.	X	X		X	
	Collector-browser	*Bareoptera roria*		X		X	X
	Collector-browser	*Confluens hamiltoni*					X
	Predator	*Costachorema xanthopterum*				X	X
	Predator	*Costachorema callistum*			X	X	X
	Predator	*Costachorema hecton*		X		X	
	Collector-browser	*Helicopsyche* spp.		X		X	X
	Predator	*Hudsonema alienum*	X		X		
	Predator	*Hydrobiosis* (clavigera group) spp.		X		X	X
	Predator	*Hydrobiosis spatulata*	X			X	
	Predator	*Hydrobiosis* (umbripennis group) spp.	X	X	X	X	X
	Filter-feeder	*Hydrobiosella mixta*	X	X		X	X
	Predator	*Hydrochorema crassicaudatum*	X	X	X	X	X

	Predator	*Hydrochorema tenuicaudatum*	X	X	X	X	X
	Predator	*Neurochorema armstrongi*		X		X	X
	Collector-browser	*Oeconesus* spp.	X	X		X	
	Collector-browser	*Olinga* spp.	X	X		X	X
	Herb-piercer	*Oxyethira* spp.				X	
	Filter-feeder	*Orthopsyche fimbriata*	X	X	X	X	X
	Predator	*Polyplectropus* spp.	X		X		
	Predator	*Psilochorema mimicum*	X		X	X	X
	Predator	*Psilochorema macroharpax*		X		X	X
	Predator	*Psilochorema leptoharpax*				X	
	Predator	*Psilochorema nemorale*				X	X
	Collector-browser	*Pycnocentrella eruensis*		X		X	X
	Collector-browser	*Pycnocentrodes* spp.	X	X		X	
	Predator	*Philorhethrus agilis*		X	X	X	
	Shredder	*Triplectides obsoletus*		X			X
Megaloptera	Predator	*Archichauliodes diversus*		X	X	X	X
Diptera	Collector-browser	*Aphrophila* spp.	X	X	X	X	X
	Filter-feeder	*Austrosimulium* spp.	X	X	X	X	X
	Collector-browser	Chironominae spp.	X	X	X	X	X
	Collector-browser	Diamesea spp.			X		X
	Collector-browser	Orthocladinae spp.	X	X	X	X	X
	Predator	Tanypodinae spp.	X	X	X	X	
	Collector-browser	Empididae spp.	X	X	X	X	X
	Collector-browser	Eriopterini spp.	X	X	X	X	X
	Collector-browser	Hexatomini spp.	X	X	X	X	
	Shredder	*Limonia* spp.	X			X	
	Collector-browser	Muscidae spp.	X		X	X	X
	Collector-browser	*Paradixa harrisi*	X		X		
	Collector-browser	Psychodidae sp. 1	X		X		
	Collector-browser	Psychodidae sp. 2			X		
	Collector-browser	Tanyderidae spp.				X	
	Predator	Ceratopogonidae spp.	X		X		
Mollusca	Scraper	*Potamopyrgus* spp.	X	X	X	X	X
	Filter-feeder	*Sphaerium* spp.	X		X		
	Collector-browser	*Latia* spp.	X				
Coleoptera	Collector-browser	Elmidae spp.	X	X	X	X	X
	Collector-browser	Hydraenidae spp.	X	X	X	X	X
	Predator	Hydrophilidae spp.	X		X		
	Collector-browser	Ptilodactylidae spp.	X	X	X	X	X
	Collector-browser	Scirtidae spp.	X	X	X		X
Oligochaeta	Collector-browser	Oligochaeta spp.	X	X	X	X	X

Crustacea	Filter-feeder	Ostracoda spp.	X	X	X	X	X
	Shredder	*Paranephrops planifrons*	X	X	X	X	

Appendix 2 The presence (X symbol) or absence (no symbol) of aquatic macroinvertebrate orders, functional feeding groups and taxa collected from eleven streams in Canterbury (see Chapter 3).

Order	Functional Feeding Group	Taxa	Banks Stream	Knob Creek	Lower Farm Stream	Upper Motukaika River	Maungati Stream	Nimrod Stream	Little Stream	Hewsons Stream	Flynn Stream	Waimak. Trib.	Binser Stream
Ephemeroptera	Predator	*Ameletopsis perscitus*						X					
	Collector-browser	*Austroclima jollyae*	X	X								X	X
	Filter-feeder	*Coloburiscus humeralis*	X	X	X	X	X	X	X	X	X	X	X
	Collector-browser	*Deleatidium* spp.	X	X	X	X	X	X	X	X	X	X	X
	Predator	*Ichthybotus bicolor*				X		X					
	Collector-browser	*Neozephlebia scita*	X	X	X		X	X	X	X	X	X	X
	Collector-browser	*Nesameletus austrinus*		X						X	X	X	
	Collector-browser	*Nesameletus ornatus*			X								
	Collector-browser	*Nesameletus vulcanus*	X										
Plecoptera	Shredder	*Acroperla trivacuata*	X				X						
	Shredder	*Austroperla cyrene*	X				X	X			X	X	
	Collector-browser	*Cristaperla fimbria*		X	X				X	X	X		
	Collector-browser	*Halticoperla viridans*		X								X	
	Collector-browser	*Megaleptoperla* spp.				X	X	X					
	Collector-browser	*Spaniocerca zelandica*		X	X				X	X	X	X	
	Predator	*Stenoperla prasina*	X		X	X	X	X	X	X	X	X	X
	Collector-browser	*Taraperla* spp.					X	X			X		
	Collector-browser	*Zelandobius* spp.	X	X	X	X	X	X	X		X	X	X

	Collector-browser	*Zelandoperla* spp.			X	X		X					X
Trichoptera	Filter-feeder	*Aoteapsyche* spp.	X	X	X	X	X	X	X	X			X
	Collector-browser	*Allocentrella magnicornis*										X	
	Collector-browser	*Bareoptera roria*	X	X	X	X		X			X		X
	Collector-browser	*Confluens olingoides*							X			X	
	Predator	*Costachorema* spp.				X		X			X	X	
	Predator	*Edpercivalia maxima*		X								X	
	Collector-browser	*Helicopsyche* spp.		X	X	X	X	X		X	X	X	X
	Predator	*Hudsonema* spp.	X	X	X		X	X	X	X	X	X	
	Predator	*Hydrobiosis* spp.	X	X	X	X	X	X	X	X	X	X	X
	Filter-feeder	*Hydrobiosella mixta*	X	X	X	X	X		X		X	X	X
	Predator	*Hydrochorema crassicaudatum*		X								X	
	Predator	*Hydrochorema tenuicaudatum*									X	X	X
	Predator	*Neurochorema confusum*				X		X					
	Predator	*Neurochorema forsteri*						X					
	Collector-browser	*Oeconesus* spp.	X	X			X				X	X	
	Collector-browser	*Olinga* spp.	X	X	X	X	X	X	X	X	X	X	X
	Herb-piercer	*Oxyethira* spp.		X			X		X	X	X	X	
	Predator	*Polyplectropus* spp.	X		X			X		X			
	Predator	*Psilochorema tautoru*					X		X				
	Predator	*Psilochorema macroharpax*	X		X	X	X	X			X		X
	Predator	*Psilochorema leptoharpax*	X			X							X
	Predator	*Psilochorema*	X			X	X	X	X	X	X		

		bidens											
	Collector-browser	*Pycnocentria* spp.	X	X			X	X		X	X	X	X
	Collector-browser	*Pycnocentrodes* spp.	X	X	X	X	X	X	X	X	X	X	X
	Predator	*Philorheithrus agilis*	X	X		X			X			X	
	Shredder	*Triplectides obsoletus*							X				
	Collector-browser	*Zelolessica meizon*										X	
Mecoptera	Predator	*Nannochorista philpotti*	X	X			X	X	X				
Megaloptera	Predator	*Archichauliodes diversus*	X		X	X	X	X	X	X	X		X
	Collector-browser	*Aphrophila neozelandica*	X	X	X	X		X	X		X	X	X
	Filter-feeder	*Austrosimulium* spp.	X	X	X	X	X	X	X	X	X	X	X
	Collector-browser	Chironominae spp.	X	X	X	X	X	X	X	X	X	X	X
	Collector-browser	Diamesea spp.	X		X		X	X	X	X	X	X	X
	Collector-browser	Orthocladinae spp.	X	X	X	X	X	X	X	X	X	X	X
	Predator	Tanypodinae spp.	X	X	X	X	X	X	X	X	X	X	X
	Collector-browser	Empididae spp.	X	X	X	X	X	X	X		X	X	X
	Collector-browser	Eriopterini spp.	X	X	X	X	X	X		X			X
Diptera	Collector-browser	Ephydridae spp.							X	X			
	Collector-browser	Hexatomini spp.	X	X	X	X				X	X		X
	Shredder	*Limonia* spp.	X									X	
	Collector-browser	Muscidae spp.	X	X	X		X		X	X	X	X	
	Collector-browser	*Nothodixa* spp.	X	X	X		X	X	X	X	X	X	
	Collector-browser	*Paradixa* spp.								X			
	Collector-browser	*Paralimnophila skusei*				X							
	Collector-browser	Psychodidae sp. 1	X						X	X	X	X	
	Collector-browser	Psychodidae: *Phlebotomine* spp.					X						

	Predator	Sciomyzidae spp.					X							
	Predator	Tabanidae spp.				X		X	X					
	Collector-browser	Tanyderidae spp.	X				X	X				X	X	
	Predator	Ceratopogonidae spp.	X	X	X	X	X	X	X			X	X	X
	Collector-browser	*Zelandotipula* spp.					X							
	Scraper	*Gyraulus* spp.											X	
Mollusca	Scraper	*Potamopyrgus* spp.	X	X	X	X	X	X	X	X		X	X	X
	Filter-feeder	*Sphaerium* spp.	X				X					X		
	Predator	*Berosus* spp.										X		
	Collector-browser	Elmidae spp. (larvae)	X	X	X	X	X	X	X	X		X	X	X
	Collector-browser	Elmidae spp. (adult)				X	X	X		X			X	
Coleoptera	Collector-browser	Hydraenidae spp. (adult)	X	X		X	X	X	X	X		X	X	X
	Predator	Hydrophilidae spp.					X					X	X	X
	Collector-browser	Ptilodactylidae spp.	X				X		X				X	
	Collector-browser	Scirtidae spp.	X	X			X					X	X	
	Predator	Dytiscidae spp.					X							
Hemiptera	Herb-piercer	*Sigara* spp.								X				
Tricladida	Predator	Tricladida spp.	X	X	X	X	X						X	X
Oligochaeta	Collector-browser	Oligochaeta spp.	X	X	X	X	X	X	X	X		X	X	X
Crustacea	Filter-feeder	Ostracoda spp.	X	X	X	X	X	X	X	X		X	X	X

Appendix 3 The presence (X symbol) or absence (no symbol) of aquatic macroinvertebrate orders, functional feeding groups and taxa collected from four Canterbury streams. Surveys of macroinvertebrates were conducted once and then six weeks after at control sites where no leaves were added to the stream (top table), and at sites where leaf litter was added weekly (bottom table; see Chapter 4).

Order	Functional Feeding Group	Taxa	No leaves added							
			Before				After			
			Lower Farm Stream	Upper Motukaika River	Maungati Stream	Binser Stream	Lower Farm Stream	Upper Motukaika River	Maungati Stream	Binser Stream
Ephemeroptera	Predator	*Ameletopsis perscitus*								
	Filter-feeder	*Coloburiscus humeralis*	4	X	X	X		X		X
	Collector-browser	*Deleatidium* spp.	X	X	X	X	X	X	X	X
	Collector-browser	*Neozephlebia scita*			X				X	
	Collector-browser	*Nesameletus austrinus*	X							
	Collector-browser	*Nesameletus ornatus*					X	X		X
Plecoptera	Shredder	*Austroperla cyrene*								
	Collector-browser	*Megaleptoperla* spp.						X		
	Collector-browser	*Spaniocerca zelandica*								
	Predator	*Stenoperla prasina*		X		X		X		
	Collector-browser	*Zelandobius* spp.	X	X		X	X			X
	Collector-browser	*Zelandoperla* spp.					X	X		X
Trichoptera	Filter-feeder	*Aoteapsyche* spp.	X			X	X	X	X	X
	Collector-browser	*Bareoptera roria*					X		X	X
	Predator	*Costachorema xanthopterum*					X			
	Predator	*Costachorema callistum*								
	Predator	*Costachorema psaropterum*				X				

	Collector-browser	*Helicopsyche* spp.		X	X			X	X	X
	Predator	*Hudsonema* spp							X	X
	Predator	*Hydrobiosis* (clavigera group) spp.	X	X		X	X	X		
	Predator	*Hydrobiosis* (umbripennis group) spp.	X	X	X	X	X	X	X	X
	Filter-feeder	*Hydrobiosella* spp				X				
	Predator	*Neurochorema confusum*						X		
	Collector-browser	*Oeconesus* spp.								X
	Collector-browser	*Olinga* spp.		X	X	X	X	X	X	X
	Herb-piercer	*Oxyethira* spp.			X				X	
	Predator	*Plectrocnemia* spp.								
	Predator	*Psilochorema* spp.		X	X	X	X	X	X	X
	Collector-browser	*Pycnocentria* spp.			X	X		X		X
	Collector-browser	*Pycnocentrodes* spp.	X	X	X	X	X	X	X	X
Mecoptera	Predator	*Nannochorista philpotti*								
Megaloptera	Predator	*Archichauliodes diversus*	X	X			X	X		X
Diptera	Collector-browser	*Aphrophila neozelandica*	X			X	X	X	X	X
	Filter-feeder	*Austrosimulium* spp.	X	X	X	X	X	X		X
	Collector-browser	Chironominae spp.	X	X	X	X	X	X		X
	Collector-browser	Diamesea spp.	X			X				
	Collector-browser	Orthocladinae spp.	X	X	X	X	X	X	X	X
	Predator	Tanypodinae spp.	X	X	X	X	X	X	X	
	Collector-browser	Empididae spp.	X	X	X	X	X			X
	Collector-browser	Eriopterini spp.	X	X		X	X	X		
	Collector-browser	Hexatomini spp.	X							

	Collector-browser	Muscidae spp.			X	X	X			
	Collector-browser	*Nothodixa* spp.			X				X	
	Predator	Tabanidae spp.								
	Collector-browser	Tanyderidae spp.								
	Predator	Ceratopogonidae spp.	X	X			X			
Mollusca	Scraper	*Potamopyrgus* spp.	X		X	X	X	X	X	X
	Predator	*Berosus* spp.								
	Collector-browser	Elmidae spp. (larvae)	X	X	X		X	X	X	X
Coleoptera	Collector-browser	Elmidae spp. (adult)		X				X	X	
	Collector-browser	Hydraenidae spp. (adult)						X		
	Collector-browser	Scirtidae spp.							X	
Tricladida	Predator	Tricladida spp.								
Oligochaeta	Collector-browser	Oligochaeta spp.	X	X	X	X	X		X	X
Crustacea	Filter-feeder	Ostracoda spp.			X				X	X

Order	Functional Feeding Group	Taxa	No leaves added							
			Before				After			
			Lower Farm Stream	Upper Motukaika River	Maungati Stream	Binser Stream	Lower Farm Stream	Upper Motukaika River	Maungati Stream	Binser Stream
Ephemeroptera	Predator	*Ameletopsis perscitus*								
	Filter-feeder	*Coloburiscus humeralis*	X	X	X	X		X	X	X
	Collector-browser	*Deleatidium* spp.	X	X	X	X	X	X	X	X
	Collector-browser	*Neozephlebia scita*			X					
	Collector-browser	*Nesameletus austrinus*	X							
	Collector-browser	*Nesameletus ornatus*					X			X
Plecoptera	Shredder	*Austroperla cyrene*		X						
	Collector-browser	*Megaleptoperla* spp.		X						
	Collector-browser	*Spaniocerca zelandica*								
	Predator	*Stenoperla prasina*		X	X			X		X
	Collector-browser	*Zelandobius* spp.	X		X	X	X	X	X	X
	Collector-browser	*Zelandoperla* spp.				X	X			X
Trichoptera	Filter-feeder	*Aoteapsyche* spp.	X			X	X	X	X	X
	Collector-browser	*Bareoptera roria*						X		X
	Predator	*Costachorema xanthopterum*								
	Predator	*Costachorema callistum*								
	Predator	*Costachorema psaropterum*				X				
	Collector-browser	*Helicopsyche* spp.		X	X			X	X	
	Predator	*Hudsonema* spp							X	X

	Predator	*Hydrobiosis* (clavigera group) spp.	X	X		X		X		
	Predator	*Hydrobiosis* (umbripennis group) spp.	X	X	X	X	X	X	X	X
	Filter-feeder	*Hydrobiosella* spp				X				
	Predator	*Neurochorema confusum*						X		
	Collector-browser	*Oeconesus* spp.								X
	Collector-browser	*Olinga* spp.		X		X	X	X		X
	Herb-piercer	*Oxyethira* spp.			X					
	Predator	*Plectrocnemia* spp.	X							
	Predator	*Psilochorema* spp.		X	X	X	X	X	X	X
	Collector-browser	*Pycnocentria* spp.	X			X		X		X
	Collector-browser	*Pycnocentrodes* spp.	X	X		X	X	X	X	X
Mecoptera	Predator	*Nannochorista philpotti*							X	
Megaloptera	Predator	*Archichauliodes diversus*	X	X	X		X	X		X
Diptera	Collector-browser	*Aphrophila neozelandica*	X	X		X	X	X		X
	Filter-feeder	*Austrosimulium* spp.	X	X	X	X	X	X		
	Collector-browser	Chironominae spp.	X	X	X	X	X	X		X
	Collector-browser	Diamesea spp.	X		X	X				
	Collector-browser	Orthocladinae spp.	X	X	X	X	X	X	X	X
	Predator	Tanypodinae spp.	X	X	X	X	X		X	
	Collector-browser	Empididae spp.	X	X		X	X			X
	Collector-browser	Eriopterini spp.	X	X		X			X	X
	Collector-browser	Hexatomini spp.								
	Collector-browser	Muscidae spp.			X	X				
	Collector-browser	*Nothodixa* spp.	X		X				X	X

	Predator	Tabanidae spp.		X						
	Collector-browser	Tanyderidae spp.							X	
	Predator	Ceratopogonidae spp.	X	X			X			
Mollusca	Scraper	*Potamopyrgus* spp.	X		X	X	X	X	X	X
	Predator	*Berosus* spp.							X	
	Collector-browser	Elmidae spp. (larvae)	X	X	X		X	X	X	X
Coleoptera	Collector-browser	Elmidae spp. (adult)								X
	Collector-browser	Hydraenidae spp. (adult)		X				X		X
	Collector-browser	Scirtidae spp.								
Tricladida	Predator	Tricladida spp.								
Oligochaeta	Collector-browser	Oligochaeta spp.	X	X	X	X	X		X	X
Crustacea	Filter-feeder	Ostracoda spp.			X				X	